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CORRIGENDA

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Page 289: Equation (7) should read:

$$\delta_1 = r + \rho \log_e (N/K). \quad \ldots\ldots\ldots\ldots (7)$$

Page 291: Equation (12) should read:

$$N_2 = n_1 (N_2/n_1)^{r_2/r_1}, \quad \ldots\ldots\ldots\ldots (12)$$

THE COPPER CONTENT OF THE LIVER AND BLOOD OF SOME VERTEBRATES

By A. B. BECK*

(*Manuscript received August* 3, 1955)

Summary

Determinations have been made of the concentration of copper in the blood and liver from a wide range of vertebrate species.

The blood copper levels show trends which do not follow the phylogenetic relationships implied in current systems of classification. The highest levels are found in the pig (1.4 mg copper/l whole blood), and the lowest in the domestic fowl and turkey (0.23 mg/l). Marsupials show low values (0.3-0.4 mg/l), whereas in most other species the values lie between 0.5 and 1.0 mg/l. It is suggested that the usual range in an individual species represents the optimum for the physiological requirements of this species.

The concentration of copper in the liver of most species lies below 50 p.p.m. copper on a dry weight basis. High values are found in the ruminant, the duck, the frog, and in certain fish. From a consideration of the data presented, it seems probable that the high liver copper level characteristic of some species is due, not to a higher intake of copper or to a greater absorption, but to a lesser ability to restrict the storage of copper in the liver.

Although there is no suggestion of sex difference in liver copper levels of most species, a highly significant difference ($P < 0.001$) has been noted in the Australian salmon (*Arripis trutta* Bloch & Schneider).

I. INTRODUCTION

A recent review by Underwood (1953) has shown the paucity of information on the copper levels in the liver and blood of vertebrates except in a few species which have been studied in detail. Relatively little new information has appeared since the review by Elvehjem (1935) and, furthermore, much of the earlier work is of limited value because of doubtful analytical methods, particularly in the case of blood.

As early as 1931 Cunningham showed that the copper level in the liver of sheep and cows was much higher than in certain other species. This fact generally has been ignored and no attempt seems to have been made to assess its significance.

The present investigation has been carried out to extend Cunningham's observations by examination of the liver and blood of as wide a range of species as was available in Western Australia. It was designed to ascertain if systematic variations of copper levels occurred in the different classes and orders of vertebrates and to provide basic data necessary for a proper study of the comparative biochemistry of copper. It was also hoped that some light would be thrown on the anomalous copper status of the sheep and the cow.

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The present paper includes data from adult non-pregnant animals only, as numerous workers have shown that the pattern of copper metabolism is different in pregnant animals and in the embryo.

II. Material Studied

Samples of liver and blood from horses, pigs, and poultry were obtained from slaughter-house material. Blood was collected from the carotid artery. The values for sheep were obtained both from experimental animals, and from animals slaughtered for rations. Wild species were usually obtained by shooting, and where it was possible to obtain blood samples these were obtained by puncture of the heart or of adjacent arteries. The samples from "Ord River" are from country adjacent to the Kimberley Research Station, some 45 miles east of Wyndham. The specimens of the giant toad (*Bufo marinus* L.) were obtained by air freight from the canefields of Queensland.

The whale liver samples were obtained from dead animals on the flensing decks of the whaling companies operating in Queensland and Western Australia. In all cases the animals had been dead for at least 3 hr and the "blood" sample, obtained by cutting arteries in the snout, consisted of a variable mixture of whole blood and serum or plasma. Iron determinations were done on these samples to obtain some indication of the amount of red cells present.

Although there is no suggestion that normal seasonal variations in diet have any significant effect on levels of copper in blood or liver, the date of sampling is indicated for all wild species. Such dates have been omitted from domestic, commercial, or laboratory animals which exist on a more uniform diet.

The classifications of Simpson (1945) have been followed in the arrangement of results. In naming fish, the papers of Whitley (1940, 1948), Olsen (1953), and Thomson (1954) have been followed.

III. Analytical Methods

Copper determinations were made by means of the diethyldithiocarbamate complex in amyl alcohol after destruction of organic matter by nitric, sulphuric, and perchloric acids (Eden and Green 1940).

Where haemoglobin levels are reported, they are calculated from iron content which was estimated by the dipyridyl method (Jackson 1938). It has been assumed that blood contains 1 per cent. non-haemoglobin iron and that haemoglobin contains 0.34 per cent. iron.

In the present investigation the results for liver copper values are subject to errors from two sources. The first is due to an uneven distribution of copper in the liver: duplicate samples from the same liver of whales, kangaroos, birds, crocodiles, and fish have given results which may differ by up to 20 per cent. although the difference is usually less.

This source of error particularly applies to the wallaby livers from Ord River where transport difficulties made it necessary to collect small samples (1-3 g dry weight) ; it also applies in the case of whales, where, of necessity, only a small portion of the liver was taken for analysis. In most cases, however, a fairly large portion of the liver was taken, dried, and subsampled. With smaller animals the whole liver was analysed.

The second source of error is due to the presence of variable amounts of fat in the liver. This acts as a diluent, and lowers the concentration of copper in the tissues. With mammals the percentage of fat is normally quite low, and no correction has been made for fat content. Only three mammalian livers (two cat and one leopard seal) were noted to be obviously fatty, and in these cases the results were recalculated to a basis of 5 per cent. fat. Bird livers normally show no obvious signs of fat although one batch of livers from domestic fowls was noted to be very fatty. The copper content of this batch was calculated to a basis of 15 per cent. fat which was the mean level in a random selection of "non-fatty" livers from fowls.

In the case of reptiles, amphibia, and fish, the percentage of fat in the liver is extremely variable, and may rise to high levels. In earlier samples such fatty livers were extracted with petroleum ether, and the determination of copper was made on the fat-free residue. Subsequently, in tests on very fatty frog and fish livers it was found that some copper (up to 10 per cent.) was dissolved by the petroleum ether. Although this error is of no great consequence, in all later samples from reptiles, amphibia, and fish, the dried liver was extracted with petroleum ether by standing and decantation until fat-free. The percentage of fat-free material was thus obtained, and both this material and the extracted fat were digested together for copper estimation. In the results for reptiles (see Appendix 1) where no comment is made, the samples were not obviously fatty, and analysis is on the dry liver without correction for fat content.

The blood was usually obtained with a stainless steel needle and an all-glass syringe. The brass butts of the needles were removed, and the needles were mounted in heavy rubber tubing. During the course of the investigation it was found that some stainless steel needles contained copper, and that appreciable amounts (up to 2 μg) could dissolve during the passage of blood through the needle. Subsequently all needles were tested by soaking for several hours in dilute ammonia solution; the addition of a solution of sodium diethyldithiocarbamate showed if copper was present. The blood samples from marsupials and the wild turkey, taken between Ord River and Port Hedland, were obtained with needles which were no longer available for testing when this source of error was discovered. However, as the results for these marsupials are the same as, or even lower than, results for similar species elsewhere it is fairly certain that no contamination has occurred.

TABLE 1

THE COPPER CONTENT OF THE LIVER AND BLOOD OF ADULT ANIMALS

Values from published papers. Liver values as p.p.m. copper on dry weight basis; blood values as mg copper/l on whole blood

Species	Blood Copper (mg/l)	Liver Copper (p.p.m.)
Man		
Male	0.96 ± 0.13[b]	25[a]
	1.01 ± 0.02[c]	24[d]
Female	1.00 ± 0.11[b]	—
	1.07 ± 0.02[c]	—
Rat	0.99[e]	12 — 18[e]
	—	10[a]
	—	11[f]
	—	34 ± 2.9[h]
Rabbit	0.69 — 0.86[g]	9[a]
	—	23 ± 3.6[h]
Guinea pig	—	17[a]
	—	23 ± 3.5[h]
Badger	—	22[a]
Pig	1.54 — 1.66[i]	41[a]
	—	21[d]
	—	15 — 20[j]
Sheep	0.4 — 1.6[k]	237[a]
	—	190 — 446[n]
Cow	0.7 — 1.7[k]	161 — 200[l]
	1.3 — 1.5[l]	77[a]
	—	70[d]
Horse	—	15[a]
	—	21[d]
Domestic fowl	—	12[a]
	—	18[d]
Fish		
Various species*	—	149 — 333[m]
Herring	—	14[a]
Torpedo marmorata	0.48 — 0.74[o]	—
Salmo trutta	—	982 ± 147[p] (range 165 — 1470)

* These values are on fat-free, dry weight basis.

[a] Cunningham (1931). [b] Lahey *et al.* (1953). [c] Sachs *et al.* (1943). [d] Elvehjem (1935). [e] Boyden, Potter, and Elvehjem (1938). [f] Lindow, Peterson, and Steenbock (1929). [g] Fontaine and Leloup (1946). [h] Lorenzen and Smith (1947). [i] Schultze, Elvehjem, and Hart (1936). [j] Harvey (1952). [k] Beck (1941). [l] Sahai and Kehar (1951). [m] Baldassi and Vignato (1942). [n] Albiston *et al.* (1940). [o] Leloup (1949). [p] Dewey, D. W., and Nicholls, A. G. (unpublished data 1955).

IV. RESULTS

The results for the copper content of liver and blood of the species examined are set out in Appendices 1 and 2 respectively. The figures are

generally presented as the mean, together with the standard deviation of the mean, and the range of the observations. Standard deviations are not given when the number of observations is less than four.

A selection of data from the literature is given for comparison in Table 1.

V. Discussion

(*a*) *Blood Copper Levels*

In the few cases where it is possible to make comparisons with other workers, the agreement is fairly close. Because of difficulties of collection, and because many of the earlier samples were collected with defective needles, the number of observations is not as great as is desirable.

The very low haemoglobin levels of the coelacanth blood suggest that it may not have been an entirely normal sample.

There seem to be no figures published for the copper content of the whole blood of birds, but Warburg and Krebs (1927) and Locke, Rosbash, and Shinn (1934) report low serum levels. The statement by Underwood (1953) that "in birds there is a striking concentration of copper in the nucleated red blood cells" seems to have been made with little real evidence, but it may be noted that in three blood samples from domestic turkeys the mean copper level of the whole blood was 0.22 mg copper/l while the corresponding figure for plasma was 0.11.

In an earlier investigation (Beck 1941) blood copper values as low as 0.4 mg/l were found in so-called "normal" sheep. It is now considered that levels of about 0.8 mg/l represent the lower limit of normality. Values between 0.4 and 0.8 are occasionally found in apparently normal sheep but these appear to indicate either an incipient copper deficiency or the presence of some factors causing a derangement of copper metabolism.

The blood copper levels show some curious variations which do not parallel the phylogenetic relationships implied in current systems of classification. Among placental mammals, the pig shows uniformly high values (1.4-1.5 mg copper/l). The rat, sheep, cow, and man show intermediate levels (*c.* 1 mg/l), while relatively low levels occur in the guinea pig and the rabbit (0.5-0.7 mg/l). Insufficient figures are available to draw any conclusions about Carnivora. Large marsupials show low values (0.3-0.4 mg/l). Still lower values are obtained from the fowl and the domestic turkey (generally 0.2-0.3 mg/l). These samples were collected from healthy commercial birds, and the possibility of a deficient copper intake is extremely improbable. The duck and the Antarctic birds show slightly higher levels, while in the emu and the wild turkey (one value only) the blood copper is within the range of the higher mammals. The limited number of fish, reptile, and amphibian bloods generally show values within this range.

There is no suggestion from this or other investigations that, for animals on diets of normal copper content, the blood copper levels are determined by dietary copper. Thus, the groups showing the highest and lowest values (the pig and the fowl respectively) are fed commercially on very similar diets. It is probable, however, that all species will show lowered blood copper levels when fed on diets which are extremely low in copper.

In the species which have been studied in detail, there is considerable evidence to show that the concentration of copper in blood can be altered markedly by physiological and pathological conditions (see review by Cartwright 1950). Thus, in man, it has been shown by numerous workers that during pregnancy there is a large rise in maternal blood copper whereas the foetal blood copper is low. In the sheep, there is no change in maternal blood copper but high levels are observed in the new-born lamb (McDougall 1947). Infections of various kinds cause a rise of levels in man; similar rises have been observed by the author in a limited number of cases in sheep, pigs, and kangaroos. In some species, haemorrhage causes increased levels (Warburg and Krebs 1927), and severe exercise causes rises in the blood copper of sheep (Dick 1954*b*) and of man (Daum 1949). Lowered levels occur in the nephrotic syndrome and in Wilson's disease. Thyroid activity also influences blood copper levels (Fontaine and Leloup 1946, 1947; Daum 1951).

Although no explanation can be given for these variations, it seems likely that they have some physiological significance. The fact that blood copper levels can vary so readily may possibly provide the clue to the differences between species. As a tentative hypothesis it is suggested that the level of copper usually encountered in the blood of healthy members of any species is determined solely by the physiological requirements of that species.

(*b*) *Liver Copper Levels*

In this investigation the values found agree closely with the relevant data of other investigators except in the case of the guinea pig. No explanation can be given for this one particular difference.

The sex difference in the liver values of the Australian salmon (*Arripis trutta* Bloch & Schneider) was highly significant ($P < 0.001$) in both 1953 and 1954. In the closely related ruff (*A. georgianus* Cuv. & Val.) the number of male livers analysed was quite small but the results did not suggest any similar difference. In no other animal species was there any evidence of sex difference.

The values for the toad (*Bufo marinus*) show a very wide variation for which no satisfactory explanation can be given.

A consideration of the data in Appendix 1 shows that the liver copper of most species lies below 50 p.p.m., and that very much higher values are found only in totally unrelated species: the ruminant, the duck, the frog,

and certain species of fish. Intermediate levels have been found in the guinea pig, in some fish, and possibly among Carnivora. While no explanation for these differences can be made at present there are several points which may be stressed.

In a study of this type, most of the livers are from animals of unknown dietary history, but the results suggest that dietary copper is not an important factor in determining liver copper levels. It is usual for fowls and ducks from commercial flocks to be fed similar diets, and yet the mean liver copper of the former is low (15 p.p.m.) and the latter is high (153 p.p.m.). The whale shows low copper levels (21 p.p.m.) in spite of the fact that the diet consists entirely of Crustaceae which presumably contain fairly large amounts of copper derived from their respiratory pigment haemocyanin. In certain parts of the Wiluna area of Western Australia the natural herbage is high in copper (10-20 p.p.m. on dry material). Sheep grazing in these areas show high liver copper values (up to 2700 p.p.m.), yet kangaroos grazing on the same areas show liver values of only 13-17 p.p.m. Diets abnormally high or low in copper will cause corresponding changes in the concentration of copper in the liver of most, if not all, species; nevertheless, there is evidence from this and other work to show that for some species the copper intake may vary within fairly wide limits without a corresponding change in liver levels. Thus, kangaroos grazing on the copper-deficient coastal areas between Gingin and Yanchep show values which are no lower than those from normal areas or from the high-copper Wiluna area. Kangaroos are not restricted in their grazing, as are sheep, but some differences in liver copper levels would be expected if these were determined by the copper content of the herbage. The work of Cunningham (1931) with rats and domestic fowls also suggests that moderate increases in dietary copper will have little effect on the liver copper levels of these two species.

The sheep and the cow are different from most other mammalian species in that, within the normal range of diets, the concentration of copper in the liver varies with the intake. Dick (1954*a*) has shown, for crossbred sheep in pens, that the liver storage is directly proportional to the intake when the dietary copper lies between 4 and 18 mg daily. Under field conditions in Western Australia, there is generally a good correlation between liver copper levels and the copper levels of pastures in the growing period. Less information is available concerning the cow, but experience in the areas of copper deficiency has shown that the levels of copper in the liver follow the levels in the pasture (Bennetts *et al.* 1941, 1948). Under conditions of high copper intake, the cow appears to have a greater ability to regulate liver storage than the sheep. The work of Cunningham (1946) with cows showed that daily doses of copper sulphate, at the rate of 0.3-0.5 mg copper/lb live weight for 5-11 months, had no untoward effect on the animals and the liver copper was raised to only 570 p.p.m. In the experiments of Dick (1954*a*) a group of five sheep

received 33.6 mg copper daily (approx. 0.45 mg copper/lb live weight) for a period of 5½ months; two sheep died from copper poisoning after 5 months, and the mean liver copper of the remaining sheep was 2340 p.p.m. at the conclusion of the experiment.

The development of high liver copper levels on diets of normal copper content could be due either to increased absorption or decreased excretion. Although the sheep is characterized by high liver copper levels, there is little evidence to support the idea of excessive absorption in this species. In a large series of experiments Dick (1954*a*, 1954*b*) has shown that, on relatively high intakes of copper (10-30 mg per day), the liver storage is between 3 and 4 per cent. of the copper ingested. Urinary copper is extremely small, and unpublished figures obtained by the author show values below 10 μg/l. On the other hand, the rat maintains a low liver copper level in spite of a relatively high absorption of copper from the diet. Values obtained by Cunningham (1931) show that rats receiving a diet low in copper excrete some 26 per cent. of dietary copper in the urine. Lindow, Peterson, and Steenbock (1929) obtained similar results with rats on a normal diet.

It should be noted also that the rat is extremely tolerant to high doses of copper. Cunningham (1931) found that growth and reproduction was possible in rats fed 7.5 mg copper daily (approx. 500 p.p.m. copper in diet). By contrast, the sheep is very susceptible to increases of dietary copper, and if this is raised above about 20 mg daily (i.e. 20 p.p.m. copper in diet) excessive accumulation of copper occurs in the liver and copper poisoning may occur. The pig is another animal with a low liver copper level, and recent work has shown that normal growth and development will occur when diets containing 250 p.p.m. copper are fed (Barber, Braude, and Mitchell 1955*a*, 1955*b*; Bowler *et al.* 1955).

An explanation of the above observations may be offered in terms of differences in ability to restrict the storage of copper in the liver, due to differences in the avidity of the liver cells for copper or in the ability of the animals to excrete stored liver copper. Appropriate data to check this are not available for the rat, but Dick (1954*b*) has given pertinent values for another animal of low liver copper level, the rabbit. In his experiments, rabbits were given daily intravenous injections of 100 and 500 μg copper (as lactate) for 209 days. At the end of the period, the mean liver copper level of the control group was 7 p.p.m., of the group receiving 100 μg copper only 10 p.p.m., and of the highest copper group, 62 p.p.m.

Comparable experiments with the sheep do not seem to have been carried out, but the following balance experiment by the author is of interest. A sheep was given an intravenous injection of 20 mg copper; a fortnight later the dose was repeated. Four similar doses were then

given at weekly intervals, and the animal was slaughtered. Faeces and urine were collected throughout the experiment. Of the 120 mg of copper injected, 104 mg was retained in the body, and at least 70 per cent. of this was found in the liver.

A consideration of the data available for the sheep, rat, and rabbit suggests strongly that the development of the characteristically high liver copper level of the sheep is due to a lesser ability to restrict the storage of copper in the liver rather than to the absorption of excessive amounts. If this hypothesis applies to other species with high liver copper levels, it would be expected that the duck would be more susceptible to increases of dietary copper than the domestic fowl, and experiments are being carried out to investigate this point.

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Appendix 1

CONCENTRATION OF COPPER IN LIVERS

Values as p.p.m. on dry weight basis. S.D. not given when number of observations less than four

Species	Details	No. of Observations	Liver Copper (p.p.m.) Mean and S.D.	Liver Copper (p.p.m.) Range
PRIMATES				
Orang-outang (*Pongo pygmaeus* Hoppius)	Zoological gardens, died from unknown causes, no obvious pathological changes	1	—	27
RODENTIA				
White rat (*Rattus norvegicus* Erxleben)	Laboratory animals	5	13.2 ± 0.5	12-15
Guinea pig (*Cavia porcellus* Pall.)	Laboratory animals	33	77.3 ± 5.6	29-205
LAGOMORPHA				
Wild rabbit (*Oryctolagus cuniculus* L.)	Beverley, Narrogin, Kojonup, and Borden; July-Aug. 1952	7	15.8 ± 0.6	14-19
Rabbit (*O. cuniculus*)	Laboratory animals	4	14 ± 3	9-20
CARNIVORA				
Cat (*Felis catus* L.)	Mongrels	6	49 ± 11	9-75
Dog (*Canis familiaris* L.)	Mongrels	3	80	22-154
Fox (*Vulpes vulpes* L.)	South Merredin, Mar. 1953	3	32	23-44
Elephant seal (*Macrorhinus proboscideus* Peron & Lesueur)	Heard I., Feb. 1954 and 1955. One male, nine females	10	66 ± 6	34-90
Leopard seal (*Hydrurga leptonyx* Blainville)	Heard I., Feb. 1955, males	2	95	84-105
Weddell seal (*Leptonychotes weddellii* Lesson)	Sandefjord Bay, Antarctica, Feb. 1955, females	3	38	24-46
PERISSODACTYLA				
Horse (*Equus caballus* L.)		6	14.8 ± 1.1	12-19
ARTIODACTYLA				
Pig (*Sus scrofa* L.)	Toodyay district	14	18.9 ± 0.9	15-25
Goat (*Capra hircus* L.)	Pt. Hedland district, Sept.-Nov. 1954	6	300 ± 62	157-590
Sheep (Merino) (*Ovis aries* L.)	(*a*) Beverley, dry grazing, Apr.-May 1952	6	329 ± 47	140-451
	(*b*) Beverley, green herbage, June-Nov. 1952	21	298 ± 28	123-584
	Mean of (*a*) and (*b*)	27	305 ± 24	123-584

APPENDIX 1 (*Continued*)

Species	Details	No. of Observations	Liver Copper (p.p.m.) Mean and S.D.	Range
CETACEA				
Humpback whale (*Megaptera nodosa* Bonnaterre)	(*a*) Carnarvon, W.A., June 1952	13	18.9 ± 1.2	15-30
	(*b*) Pt. Cloates, W.A., Aug. 1952	16	20.4 ± 1.3	12-32
	(*c*) Brisbane, Qld., Sept. 1954	8	25.6 ± 2.2	18-38
	Overall mean (*a*)-(*c*)	37	21.0 ± 0.9	12-38
MARSUPIALIA				
Grey kangaroo (*Macropus ocydromus* Gould)	(*a*) Darkan, June 1951	2	20	—
	(*b*) Margaret R. area, May-Oct. 1952	7	18.9 ± 0.8	15-21
	(*c*) Pingrup area, Sept. 1952	4	16.7 ± 0.6	15-18
	(*d*) Kojonup area, Nov. 1952	2	22	19-26
	(*e*) Gingin-Yanchep area, Dec. 1952 and Apr. 1954	2	22	20-24
	Overall mean (*a*)-(*e*)	17	19.3 ± 0.7	15-26
Red kangaroo (*M. rufus* Desmarest)	(*a*) Merredin, July 1949	1	—	9
	(*b*) Pt. Hedland district, June 1952	3	13	13-14
	(*c*) Albion Downs station, Wiluna, July 1953	6	15.5 ± 0.4	14-17
	(*d*) Lorna Glen station, Wiluna, July 1953	2	13.5	13-14
	(*e*) Cue, Mar. 1954	1	—	16
	Overall mean (*a*)-(*e*)	13	14.2 ± 0.6	13-17
Euro (*M. robustus* Gould)	(*a*) Pt. Hedland district, June 1952	6	13.0 ± 1.0	10-17
	(*b*) Albion Downs station, Wiluna, July 1953	3	15	12-17
	Overall mean (*a*) and (*b*)	9	13.6 ± 0.8	10-17
Wallaby (*M. agilis* Schwarz)	(*a*) Ord R., June 1952	10	16.3 ± 0.7	14-20
	(*b*) Gogo station, Fitzroy R., June 1952	3	15.3 ± 0.3	15-16
	(*c*) Ord R., Dec. 1952-Jan. 1953	9	16.6 ± 0.7	14-20
	(*d*) Ord R., June 1953	13	18.3 ± 0.6	15-21
	Overall mean (*a*)-(*d*)	35	17.0 ± 0.4	14-21
Brush wallaby (*M. irma* Jourdan)	Bindoon, July 1952	1	—	19
Tammar (*Thylogale eugenii* Desmarest)	Recherche Archipelago, Feb. 1954	2	18.5	15-22

APPENDIX 1 (*Continued*)

Species	Details	No. of Observations	Liver Copper (p.p.m.) Mean and S.D.	Range
Quokka (*Setonyx brachyurus* Quoy & Gaimard)	(*a*) Laboratory animals	4	16.5 ± 0.9	14-18
	(*b*) Rottnest I., Dec. 1952	9	13.7 ± 0.8	9-17
	(*c*) Rottnest I., Nov. 1953	5	11.0 ± 0.5	10-13
	(*d*) Bald I., June 1954	2	9	8-10
	Overall mean (*a*)-(*d*)	20	13.1 ± 0.7	8-18
Rock wallaby (*Petrogale hacketti* Thomas)	Recherche Archipelago, Feb. 1954	1	—	23
Rat kangaroo (*Bettongia penicillata* Gray)	Narrogin-Williams district, Aug. 1954	2	27	21-33
AVES				
Domestic fowl (*Gallus gallus* L.)	(*a*) Australorp pullets, Mar. 1952	12	12.7 ± 0.5	9-15
	(*b*) Australorp pullets, July 1952	7	15.1 ± 0.7	13-18
	(*c*) Australorp adult birds*	10	15.1 ± 0.6	12-18
	(*d*) White leghorn cockerels	4	14.2 ± 0.5	13-15
	(*e*) White leghorn hens, 1 year culls	10	17.0 ± 1.6	14-31
	(*f*) White leghorn hens, 2 year	4	14.5 ± 0.6	13-16
	(*g*) Australorp × white leghorn hens	4	14.7 ± 0.5	14-16
	Overall mean (*a*)-(*g*)	51	14.8 ± 0.4	9-31
White muscovy duck (*Cairina moschata* L.)	(*a*) All female	12	164 ± 33	82-500
	(*b*) 7 female, 3 male	10	63 ± 7	37-102
	(*c*) All male	12	218 ± 39	88-555
	Overall mean (*a*)-(*c*)	34	153 ± 21	37-555
Turkey (*Meleagris gallopavo* L.)		6	13.5 ± 0.2	13-14
Crow (*Corvus cecilae* Mathews)	Ord. R., June 1952	6	41 ± 5	25-56
Little corrella (*Kakatoë sanguinea* Gould)	Ord. R., June 1952	3	16	16-17
Galah (*K. roseicapilla* Vieillot)	Gogo station, Kimberleys, June 1952	3	17	15-19
Kite hawk (*Milvus migrans* Boddaert)	Ord R. and Pt. Hedland, June 1952	3	18	17-19
Wedgetail eagle (*Uroaëtus audax* Latham)	Ord R., June 1952	1	—	26
Brown hawk (*Falco berigora* Vigors & Horsfield)	Wiluna, July 1953	1	—	23

* Birds not laying, livers fatty, results calculated on basis of 15% fat.

APPENDIX 1 (*Continued*)

Species	Details	No. of Observations	Liver Copper (p.p.m.) Mean and S.D.	Range
Butcher bird (*Cracticus torquatus* Latham)	Perth, Sept. 1952	1	—	12
Kimberley kookaburra (*Dacelo leachi* Vigors & Horsfield)	Ord R., June 1952	1	—	26
Bee eater (*Merops ornatus* Latham)	Ord R., June 1952	2	—	15
Pied goose (*Anseranas semipalmata* Latham)	Ord R., June 1952	2	46	45-47
Wagtail (*Rhipidura leucophrys* Latham)	Perth, June 1951	1	—	29
Wild turkey (*Eupodotis australis* Gray)	Ord R., June 1952	2	31	29-33
Emu (*Dromaius novaehollandiae* Latham)	Lorna Glen station, Wiluna, Sept. 1953	4	28 ± 4	17-37
Southern skua (*Stercorarius skua lonnbergi* Mathews)	Heard I., Mar. 1954	3	18	17-20
Storm petrel (*Oceanites oceanicus* Kuhl)	Heard I., Mar. 1954	1	—	21
Giant petrel (*Macronectes giganteus* Gmelin)	Heard I., Mar. 1954, young bird	1	—	30
Rockhopper penguin (*Eudyptes chrysocome* Forster)	Heard I., Mar. 1954, Feb. 1955	6	15 ± 0.6	13-17
Macaroni penguin (*E. chrysolophus* Brandt)	Heard I., Mar. 1954, Feb. 1955	3	15	13-16
Gentoo penguin (*Pygoscelis papua* Forster)	Heard I., Mar. 1954, Feb. 1955	5	13 ± 1.5	11-19
REPTILIA				
Freshwater tortoise (*Chelodina oblonga* Gray)	Perth, Oct. 1952	1	—	34
Crocodile (*Crocodilus johnsoni* Krefft)	Ord R., June-Nov. 1952	4	17.7 ± 2.6	11-23
Brown snake ("Linga")	Ord R., Nov. 1952	1	—	45
Brown snake (*Demansia nuchalis* Guenther)	Beverley, just emerged from hibernation, Oct. 1953	1	—	40
Blue-tongued lizard (not identified)	Ord R., Oct. 1952	1	—	19*

* Livers fatty, results on fat-free basis.

APPENDIX 1 (*Continued*)

Species	Details	No. of Observations	Liver Copper (p.p.m.) Mean and S.D.	Range
Bob-tail lizard (*Trachysaurus rugosus* Gray)	(*a*) Beverley, June 1952	1	—	12
	(*b*) Perth, Oct. 1952	1	—	10
	(*c*) Merredin, hibernating, June 1953	1	—	11.5*
	(*d*) Perth, Feb. 1955	3	14*	11-16
	(*e*) Rottnest I., Feb. 1955	3	16*	11-20
	Overall mean (*a*)-(*e*)	9	14 ± 1	10-20
Skink (*Lygosoma trilineatum* Gray)	Cheyne Beach, Mar. 1953	1	—	10
Skink (*L. microtis* Gray)	Cheyne Beach, Mar. 1953	1	—	10
Skink (*Egernia napoleonis* Gray)	Cheyne Beach, Mar. 1953	1	—	10
AMPHIBIA-ANURA				
Frogs:				
Lymnodynastes d. dorsalis Gray	(*a*) Perth, Oct. 1952	1	—	865
	(*b*) Cheyne Beach, Mar. 1953	1	—	124
Hyla aurea raniformis Keferstein	Cheyne Beach, Mar. 1953	5	293 ± 58	172-454
Giant toad (*Bufo marinus* L.)	Qld., Mar. 1953 and Apr. 1954	14	468 ± 140*	10-1640
PISCES: ELASMOBRANCHII				
Blue whaler shark (*Carcharhinus mackiei* Phillips)	Rottnest I., Dec. 1952	1	—	27*
Grey nurse shark (*Carcharias arenarius* Ogilby)	(*a*) Cheyne Beach, Mar. 1953	1	—	50*
	(*b*) Denmark, W.A., Apr. 1954	1	—	35*
Gummy shark (*Emissola antarctica* Günther)	Cheyne Beach, Mar. 1953	1	—	18*
School shark (*Galeorhinus australis* Macleay)	Rottnest I., Dec. 1953	2	13	11-15*
Stingray (*Urolophus mucosus* Whitley)	Cheyne Beach, Mar. 1953	1	—	10*
Southern shovelnose ray (*Aptychotrema vincentiana* Haacke)	Cheyne Beach, Mar. 1953	1	—	13
PISCES: TELEOSTII				
Mullet (not identified)	Ord R., June 1952	1	—	335

* Livers fatty, results on fat-free basis.

APPENDIX 1 (*Continued*)

Species	Details	No. of Observations	Liver Copper (p.p.m.) Mean and S.D.	Range
Bream (*Mylio butcheri* Munro)	Swan R., Sept. 1952-Mar. 1953	5	544 ± 202	108-1260
Cobbler (*Cnidoglanis macrocephalus* Cuv. & Val.)	(*a*) Swan R., Dec. 1952	3	10	9-11
	(*b*) Cheyne Beach, Mar. 1953	1	—	11*
Sand flathead (genus *Planiplora*)	Swan R., Jan. 1953	1	—	108
Australian salmon (*Arripis trutta* Bloch & Schneider)	Cheyne Beach, Mar. 1953 and Apr. 1954			
	(*a*) Male	18	15.0 ± 1.2*	10-30
	(*b*) Female	26	45.2 ± 3.9*	20-94
Ruff (*A. georgianus* Cuv. & Val.)	(*a*) Cheyne Beach, Mar. 1953, all female	5	62 ± 11*	26-88
	(*b*) Busselton, Jan. 1954, sexes not recorded	3	36 ± 8*	22-51
	(*c*) Denmark, W.A., Apr. 1954, 1 male, 5 females	6	59 ± 7*	44-80
	(*d*) Cheyne Beach, Apr. 1954, 1 male, 4 females	5	44 ± 4*	36-55
	Overall mean (*a*)-(*d*)	19	52 ± 4*	22-88
Skipjack (*Usacaranx georgianus* Cuv. & Val.)	(*a*) Cheyne Beach, Mar. 1953	1	—	22
	(*b*) Busselton, Jan. 1954	2	23*	16-31
Flathead (*Trudis bassensis westraliae* Whitley)	Cheyne Beach, Mar. 1953	1	—	10*
Sand whiting (*Sillago bostockii* Castelnau)	Busselton, Jan. 1954	3	24*	12-40
King George whiting (*Sillaginodes punctatus* Cuv. & Val.)	Busselton, Jan. 1954	1	—	44*
Trumpeter (*Helotes sexlineatus* Quoy & Gaimard)	Busselton, Jan. 1954	2	23*	22-23
Garfish (*Reporhamphus melanochir* Cuv. & Val.)	Busselton, Jan. 1954	2	15*	14-17
Flounder (order Heterosomata)	Busselton, Jan. 1954	1	—	29*
Rock cod (family Epinephelidae)	Busselton, Jan. 1954	1	—	13*

* Livers fatty, results on fat-free basis.

APPENDIX 1 (*Continued*)

Species	Details	No. of Observations	Liver Copper (p.p.m.) Mean and S.D.	Range
Sea mullet (*Mugil cephalus* L.)	Cheyne Beach, Mar. 1954:			
	(*a*) Male	1	—	176*
	(*b*) Female	2	256*	117-395
Morwong (*Psilocranium nigricans* Richardson)	Cheyne Beach, Mar. 1954, female	1	—	59*
Coelacanth (*Latimeria chalumnae* Smith)	Madagascar:			
	(*a*) Adult male, Oct. 1954	1	—	36*
	(*b*) Adult female, Nov. 1954	1	—	47*

* Livers fatty, results on fat-free basis.

APPENDIX 2

COPPER CONTENT OF BLOOD

Values expressed as mg copper/l of whole blood. Where no details are given, these are as in Appendix 1. Species names are the same as in Appendix 1

Species	Details	No. of Observations	Blood Copper (mg/l) Mean and S.D.	Range
Rabbit	Laboratory animals, female	3	0.75	0.70-0.79
Guinea pig	(*a*) Males	15	0.49 ± 0.01	0.40-0.58
	(*b*) Females	10	0.55 ± 0.03	0.40-0.76
	Overall mean (*a*) and (*b*)	25	0.52 ± 0.02	0.40-0.76
Cat	—	4	0.99 ± 0.13	0.80-1.38
Dog	—	3	0.70	0.59-0.79
Elephant seal	—	10	1.19 ± 0.04	0.90-1.43
Leopard seal	—	2	0.80	0.78-0.82
Weddell seal	—	2	1.29	0.90-1.68
Pig	(*a*) Mt. Barker district	15	1.42 ± 0.05	1.20-1.82
	(*b*) Northam district	15	1.37 ± 0.05	1.10-1.60
	Overall mean (*a*) and (*b*)	30	1.40 ± 0.03	1.10-1.82
Sheep (Merino wethers)	Merredin			
	(*a*) June 1949	51	1.00 ± 0.02	0.76-1.35
	(*b*) Feb. 1950	69	0.98 ± 0.01	0.75-1.28
	(*c*) Apr. 1954	40	1.09 ± 0.02	0.81-1.32
	Overall mean (*a*)-(*c*)	160	1.02 ± 0.01	0.75-1.35
Horse	—	2	0.75	0.72-0.78
Whale	Carnarvon, June 1952. (Post mortem samples, mixture of plasma and blood: Haemoglobin 7.6-11.7 g/100 ml)	12	1.18 ± 0.03	1.04-1.35
Grey kangaroo	Various localities	4	0.41 ± 0.02	0.38-0.45
Red kangaroo	Various localities	8	0.35 ± 0.02	0.24-0.41

APPENDIX 2 (*Continued*)

Species	Details	No. of Observations	Blood Copper (mg/l) Mean and S.D.	Blood Copper (mg/l) Range
Euro	Pt. Hedland and Wiluna	6	0.35 ± 0.03	0.27-0.44
Wallaby	Ord R., June 1952	5	0.34 ± 0.02	0.27-0.39
Quokka	(*a*) Rottnest I., 1953	5	0.29 ± 0.04	0.16-0.42
	(*b*) Laboratory animals	2	0.43	0.33-0.52
	Overall mean (*a*) and (*b*)	7	0.33 ± 0.04	0.16-0.52
Domestic fowl	—	51	0.23 ± 0.01	0.11-0.47
Duck	—	38	0.35 ± 0.01	0.22-0.45
Turkey	—	14	0.23 ± 0.01	0.18-0.28
Emu	—	4	0.64 ± 0.03	0.55-0.71
Wild turkey	—	1	—	0.54
Giant petrel	—	1	—	0.30
Skua	—	2	0.39	0.35-0.42
Gentoo penguin	—	5	0.50 ± 0.03	0.43-0.58
Macaroni penguin	—	3	0.53	0.50-0.55
Rockhopper penguin	—	4	0.37 ± 0.02	0.32-0.43
Bobtail lizard	Perth and Rottnest I.	5	0.78 ± 0.01	0.75-0.82
Giant toad	—	8	0.46 ± 0.04	0.25-0.67
Australian salmon	Busselton, May 1954	8	0.58 ± 0.02	0.45-0.64
Ruff	Cheyne Beach and Denmark, W.A., 2 males, 9 females	11	0.71 ± 0.07	0.56-0.97
Sea mullet	—	3	0.53	0.47-0.66
Morwong	—	1	—	0.43
Coelacanth	Female (haemoglobin, 2.8 g/100 ml)	1	—	1.01

THE DISTRIBUTION AND BIOLOGY OF THE GENUS *COPTOTERMES* (ISOPTERA) IN WESTERN AUSTRALIA

By J. H. Calaby* and F. J. Gay†

(*Manuscript received July* 18, 1955)

Summary

Knowledge of the distribution and biology in Western Australia of species of *Coptotermes* has been very incomplete and in some respects erroneous, due partly to a lack of collecting and partly to the fact that the genus is notoriously difficult taxonomically.

This genus, which includes the most destructive Australian termites, is represented in the State by four species and one subspecies. The form *raffrayi* previously thought to be a good species occurring sympatrically with *acinaciformis* is shown to be a subspecies of the latter form intergrading with it through a wide zone of intermediate forms and replacing it geographically in the wetter south-western corner of the State. *C. michaelseni* is restricted to south-western Australia and previous records from South Australia, Victoria, and Queensland are shown or considered to be misidentifications of *C. frenchi*. *C. frenchi* is definitely recorded from Western Australia for the first time. The separation of these two species by microscopical measurements is discussed. The fourth species is the recently discovered and described *C. brunneus*.

The known Western Australian distributions of all species except *C. brunneus* are given. New biological data for all species are recorded, particularly on tree species attacked, dispersal of alates, and construction of mounds. *C. acinaciformis* builds symmetrical domed mounds in parts of southern Western Australia. Mound nests had not previously been recorded in the State and they differ considerably in construction from those recorded from the Northern Territory and north Queensland. *C. frenchi* is here definitely recorded as a mound builder. The mound-building habit erroneously attributed in the literature to *C. michaelseni* is shown to be due to the confusion of this species with *frenchi*.

Photographs of mounds of *C. acinaciformis raffrayi*, *C. frenchi*, and *C. brunneus* are published for the first time.

I. Introduction

Termites of the genus *Coptotermes* are widely distributed in the tropical and sub-tropical regions of the world and are particularly abundant in Australia. The economic destruction they cause greatly exceeds that of all other Australian termite genera, yet in spite of this the limits of distribution and biology of the species occurring in Western Australia are little known. This can be explained in part by a lack of collecting in the State but is also due to the great difficulty or impossibility of differentiating certain forms on soldier material, the only readily available caste of taxonomic value at the species level in the Isoptera.

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Since the latest review of the genus (Hill 1942) a considerable amount of collection and observation carried out in Western Australia has resulted in a much better idea of the distribution and biology of the various forms. This collecting has brought to light a strikingly distinct new species, a new record for the state of a known species, and new data on all species, as a result of which some of the information given in Hill's monograph needs to be modified. This includes the reduction to subspecific status of one form long thought to be specifically distinct.

The forms now known to occur in Western Australia are as follows:

C. acinaciformis acinaciformis (Froggatt), 1898. Type locality, Hall's Creek, W.A.

C. acinaciformis raffrayi Wasmann, 1900. Type locality, Swan River, W.A.

C. michaelseni Silvestri, 1909. Type locality, Mundijong, W.A.

C. frenchi Hill, 1932. Type locality, Melbourne, Victoria.

C. brunneus Gay, 1955. Type locality, 51 miles NNW. of Galena, W.A.

C. a. acinaciformis and *C. frenchi* have a wide distribution in Australia but it appears from present knowledge that the other three forms are restricted to Western Australia. For the sake of completeness it may be recalled that *C. lacteus* (Froggatt) 1898, has been recorded from Western Australia by several authors. Hill (1942, p. 162) suggests how these misidentifications may have arisen.

A representative collection of all specimens mentioned in this paper is held in the Division of Entomology Museum, C.S.I.R.O., Canberra, A.C.T.

II. C. ACINACIFORMIS ACINACIFORMIS AND C. ACINACIFORMIS RAFFRAYI (new status)

(*a*) *General and Taxonomic*

Until now authors have regarded *acinaciformis* and *raffrayi* as distinct species. Due to the difficulty of separating them on the soldier caste, much confusion has existed regarding the distribution of these two forms in south-western Australia since 1926, when Hill first recorded *acinaciformis* from the wetter parts of this region (Hill 1926). Hill (1942, p. 147) was "unable confidently to differentiate between soldiers of (these forms)" and in a footnote (p. 144) to the distribution list of *acinaciformis* indicated that some of the records based on soldier identifications "possibly refer to *C. raffrayi.*" At the same time (p. 147) he claimed that "a considerable degree of reliance" could be placed on determinations based on certain head measurements. The forms are, however, easily distinguished in the alate caste on the basis of colour. Most of the head and body is orange-yellow in *acinaciformis* and dark chestnut-brown in *raffrayi,* and the wings of *acinaciformis* are noticeably paler than those of *raffrayi.* It is emphasized

that Hill's records of the occurrence of *acinaciformis* in the wetter parts of south-western Australia were based on soldiers only, and alates of this form have never been collected in this region.

During the last few years the authors examined large numbers of soldiers of the two forms and concluded that it was not possible to make determinations on any combinations of measurements or morphological characters of this caste. No differences, other than colour in the alate caste, could be found and field observations did not demonstrate any biological differences. These facts led to the belief that the two forms were probably only subspecifically distinct and a collecting trip was therefore planned to cover areas where intergradation was likely to occur and at a time when mature alates ready for dispersal would be in the nests. These collections were compared with typical recently-collected *raffrayi* from Perth and other places in south-western Australia and with a series of typical *acinaciformis* from South Australia (Streaky Bay, 15 miles SE. of, 28.xi.1947, T. Greaves and J.H.C.) which in turn had been compared with material from Adelaide and Sydney.

Examination of this material shows clearly that *raffrayi* is only subspecifically distinct from *acinaciformis*. The south-western corner of the State is occupied by *raffrayi* to a few miles west of Lake King in the southern part of the State and a few miles east of Cunderdin along the Great Eastern Highway. All alates collected westward from these points are typical *raffrayi*. At about these points the dark chestnut-brown colour of alates begins to pale and becomes progressively paler as one proceeds east, eventually passing into the orange-yellow of typical *acinaciformis* approximately in the region of Norseman and Kalgoorlie. At the western side of this intermediate zone the transition from *raffrayi* to intermediate forms appears to be clear-cut, but at the eastern side of the cline the transition from intermediates to *acinaciformis* appears to be rather more complicated. Occasional series morphologically indistinguishable from *acinaciformis*—and hence must be considered as such—were found over large areas mixed up with intermediate forms. Further, at this eastern side one gets many colonies in which, although all alates are pale, there is a fair range of colour variation in the one nest. Because of this it is not possible to give an accurate figure for the width of the intermediate zone, but it is certainly greater than 100 miles and perhaps as wide as 200 miles. However, in view of the single character of colour on which the separation is based, it is possible that series from near the eastern edge of the intermediate zone which are morphologically indistinguishable from *acinaciformis*, may still have some tendency towards intermediacy in genetic constitution.

The distribution of *C. acinaciformis* in the southern half of Western Australia is shown on Figure 1. The heavy dotted line represents the known approximate eastern limit of the subspecies *raffrayi*.

(*b*) *Distribution Records**

(i) *Distribution of* C. a. acinaciformis (*alates or complete nest series only*).—Hall's Creek; Kalgoorlie (from Hill 1942).

Balladonia Hstd., 4 miles WSW. of, 10.xii.1953 (J.H.C.); Bardoc, 9 miles NW. of, 27.x.1954 (J.H.C. and F.J.G.); Coolgardie, 8 miles NE. of, 26.x.1954 (J.H.C. and F.J.G.); Daniell, 9 miles SW. of, 23.x.1954 (J.H.C. and F.J.G.); Daniell, 20 miles SW. of, 23.x.1954 (J.H.C. and F.J.G.); Goongarrie, 3 miles S. of, 27.x.1954 (J.H.C. and F.J.G.); Kumarl, 21 miles WNW. of, 23.x.1954 (J.H.C. and F.J.G.); Mt. Ragged, 15 miles NNW. of,

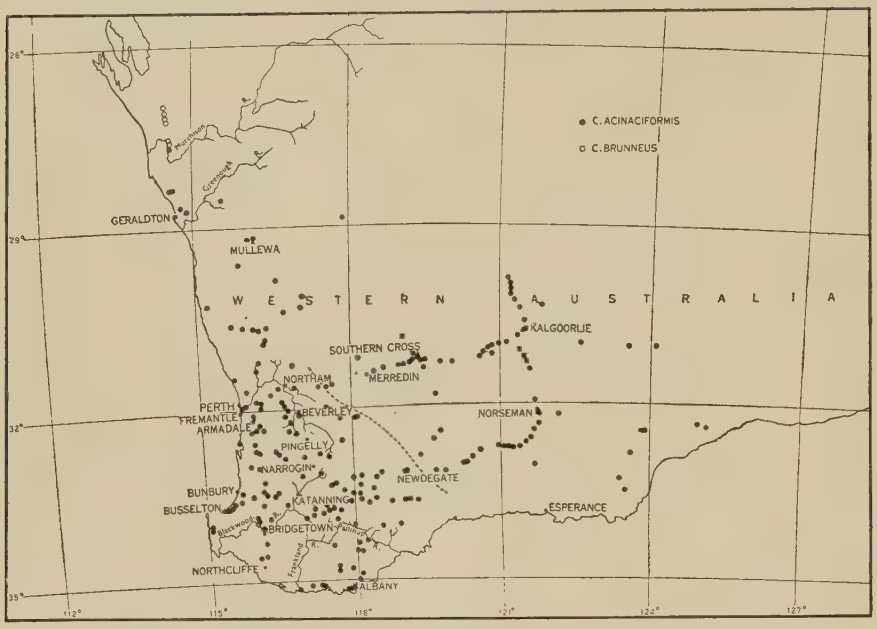

Fig. 1.—Map showing known distribution of *C. acinaciformis* (●) in southern Western Australia and known total distribution of *C. brunneus* (○). The heavy dotted line represents the known approximate eastern limit of *C. a. raffrayi*.

18.xi.1947 (T. Greaves and J.H.C.); Norseman, 21 miles E. of, 12.xi.1947 (T.G. and J.H.C.); Norseman, 11 miles SSW. of, 24.x.1954 (J.H.C. and F.J.G.); Norseman, 21 miles SSW. of, 24.x.1954 (J.H.C. and F.J.G.).

(ii) *Distribution of* C. a. raffrayi (*alates or complete nest series only*).—Ludlow; Mundaring; Pemberton; Swan River (= Perth); Wonnerup; (from Hill 1942).

Albany, 15 miles NE. of, 8.xi.1947 (T.G. and J.H.C.); Armadale, 13 miles SE. of, 2.xi.1953 (J.H.C.); Bakers Hill, 6 miles SW. of, 1.xi.1954 (J.H.C. and F.J.G.); Bindoon, 27.x.1953 (J.H.C.); Bowelling, 2 miles NW. of, 11.xi.1952 (J.H.C.); Boyanup, 3 miles S. of, 10.xi.1952 (J.H.C.);

* All records are from Western Australia unless otherwise indicated.

Brookton, 9 miles WSW. of, 20.x.1954 (J.H.C. and F.J.G.) ; Brookton, 19 miles W. of, 20.x.1954 (J.H.C. and F.J.G.) ; Cunderdin, 4 miles E. of, 1.xi.1954 (J.H.C. and F.J.G.) ; Darkan, 10 miles SE. of, 11.xi.1952 (J.H.C.) ; Donnybrook, 8 miles NE. of, 10.xi.1952 (2 series) (J.H.C.) ; Dryandra, 3 miles ENE. of, 14.x.1954 (J.H.C.) ; Dumbleyung, 7 miles SE. of, 2.xi.1953 (J.H.C.) ; Dumbleyung, 12 miles WNW. of, 2.xi.1953 (J.H.C.) ; Gundaring, 6 miles E. of, 20.x.1954 (2 series) (J.H.C. and. F.J.G.) ; Jurien Bay, 8 miles E. of, 20.xi.1954 (J.H.C.) ; Katanning, 12 miles WSW. of, 13.xi.1952 (J.H.C.) ; Katanning, 8 miles NW. of, 30.x.1953 (J.H.C.) ; Kojonup, 3 miles N. of, 30.xi.1954 (J.H.C.) ; Kukerin, 4 miles NE. of, 21.x.1954 (J.H.C. and F.J.G.) ; Kukerin, 5 miles W. of, 20.x.1954 (J.H.C. and F.J.G.) ; Lake Grace, 7 miles ESE. of, 21.x.1954 (J.H.C. and F.J.G.) ; Mt. Misery, 2 miles SE. of, 21.xi.1954 (J.H.C.) ; Newdegate, 1 mile E. of, 21.x.1954 (J.H.C. and F.J.G.) ; New Norcia, 5 miles NNE. of, 27.x.1953 (J.H.C.) ; New Norcia, 8 miles NNE. of, 27.x.1953 (J.H.C.) ; Northam, 11 miles E. of, 1.xi.1954 (J.H.C. and F.J.G.) ; Northam, 8 miles WSW. of, 1.xi.1954 (J.H.C. and F.J.G.) ; Northampton, 7 miles W. of, 28.x.1952 (J.H.C.), 29.x.1952 (J.H.C.) ; Northampton, 8 miles W. of, 26.x.1953 (J.H.C.) ; Nyabing, 4 miles N. of, 30.x.1953 (J.H.C.) ; Nyabing, 7 miles N. of, 30.x.1953 (J.H.C.) ; Nyabing, 20 miles NE. of, 1.xi.1953 (J.H.C.) ; Nyabing, 9 miles ESE. of, 1.xi.1953 (J.H.C.) ; Nyabing, 13 miles WSW. of, 30.x.1953 (J.H.C.) ; Nyabing, 16 miles WSW. of, 30.x.1953 (J.H.C.) ; Nyabing, 13 miles NW. of, 2.xi.1953 (J.H.C.) ; Ongerup, 26 miles E. of, 9.xi.1947 (T.G. and J.H.C.) ; Perth, 21.xi.1951 (T.G.) ; Perth (Nedlands), 8.xi.1953 (2 series) (J.H.C.), 9.xi.1953 (2 series) (J.H.C.), 10.xi.1953 (2 series) (J.H.C.), 1.i.1954 (J.H.C.), 2.x.1954 (J.H.C.), 10.x.1954 (J.H.C.), 19.x.1954 (J.H.C. and F.J.G.), 21.xi.1954 (J.H.C.), 15.xii.1954 (J.H.C.) ; Perth (West Leederville), 10.x.1954 (D. L. McIntosh), 19.x.1954 (D.L.M.) ; Pingrup, 17 miles E. of, 1.xi.1953 (2 series) (J.H.C.) ; Pingrup, 30 miles E. of, 31.x.1953 (J.H.C.) ; Pingrup, 36 miles E. of, 31.x.1953 (J.H.C.) ; Pingrup, 37 miles E. of, 31.x.1953 (J.H.C.) ; Pingrup, 2 miles SW. of, 1.xi.1953 (J.H.C.) ; Walebing, 5 miles ENE. of, 27.x.1953 (J.H.C.).; Walebing, 8 miles ENE. of, 27.x.1953 (J.H.C.) ; Williams, 9 miles SSE. of, 2.xi.1953 (J.H.C.) ; Williams, 20 miles NW. of, 2.xi.1953 (J.H.C.) ; Williams, 31 miles NW. of, 2.xi.1953 (J.H.C.) ; Williams, 34 miles NW. of, 2.xi.1953 (J.H.C.) ; Yarloop, 1 mile E. of, 6.xii.1947 (2 series) (J. A. Mahon).

(iii) *Distribution of* C. a. acinaciformis–C. a. raffrayi *Intermediates* (*alates or complete nest series only*).— Bardoc, 3 miles SSE. of, 27.x.1954 (J.H.C. and F.J.G.) ; Boorabbin, 14 miles E. of, 29.x.1954 (J.H.C. and F.J.G.) ; Broad Arrow, 4 miles NNW. of, 27.x.1954 (J.H.C. and F.J.G.) ; Bulla Bulling, 2 miles ENE. of, 28.x.1954 (J.H.C. and F.J.G.) ; Bulla Bulling, 5 miles WSW. of, 29.x.1954 (J.H.C. and F.J.G.) ; Bulla Bulling, 9 miles WSW. of, 29.x.1954 (J.H.C. and F.J.G.) ; Bulla Bulling, 18 miles WSW. of, 29.x.1954 (J.H.C. and F.J.G.) ; Bullfinch, 10 miles NNW. of,

30.x.1954 (J.H.C. and F.J.G.) ; Bungulla, 3 miles E. of, 1.xi.1954 (J.H.C. and F.J.G.) ; Burracoppin, 6 miles WSW. of, 31.x.1954 (J.H.C. and F.J.G.) ; Carrabin, 2 miles E. of, 31.x.1954 (J.H.C. and F.J.G.) ; Coolgardie, 9 miles NE. of, 26.x.1954 (J.H.C. and F.J.G.) ; Coolgardie, 16 miles SE. of, 26.x.1954 (J.H.C. and F.J.G.) ; Coolgardie, 7 miles W. of, 28.x.1954 (J.H.C. and F.J.G.) ; Daniell, 23.x.1954 (J.H.C. and F.J.G.) ; Daniell, 15 miles SW. of, 23.x.1954 (J.H.C. and F.J.G.) ; Goongarrie, 6 miles N. of, 27.x.1954 (J.H.C. and F.J.G.) ; Goongarrie, 9 miles S. of, 27.x.1954 (J.H.C. and F.J.G.) ; Goongarrie, 11 miles NNW. of, 28.x.1954 (J.H.C. and F.J.G.) ; Kalgoorlie, 12 miles NNW. of, 26.x.1954 (J.H.C. and F.J.G.) ; Karalee, 8 miles E. of, 29.x.1954 (J.H.C. and F.J.G.) ; Lake King, 34 miles ENE. of, 22.x.1954 (J.H.C. and F.J.G.) ; Lake King, 10 miles E. of, 22.x.1954 (J.H.C. and F.J.G.) ; Lake King, 2 miles W. of, 21.x.1954 (J.H.C. and F.J.G.) ; Mt. Ragged, 14.xii.1953 (J.H.C.) ; Moorine Rock, 3 miles ENE. of, 31.x.1954 (J.H.C. and F.J.G.) ; 90-Mile Tank (*c.* 65 miles ENE. of Lake King), 14 miles ESE. of, 22.x.1954 (J.H.C. and F.J.G.) ; 90-Mile Tank, 21 miles ESE. of, 23.x.1954 (J.H.C. and F.J.G.) ; 90-Mile Tank, 27 miles ESE. of, 23.x.1954 (J.H.C. and F.J.G.) ; 90-Mile Tank, 10 miles SW. of, 22.x.1954 (J.H.C. and F.J.G.) ; 90-Mile Tank, 23 miles SW. of, 22.x.1954 (J.H.C. and F.J.G.) ; 90-Mile Tank, 32 miles SW. of, 22.x.1954 (J.H.C. and F.J.G.) ; Noongaar, 2 miles E. of, 31.x.1954 (J.H.C. and F.J.G.) ; Noongaar, 2 miles WSW. of, 31.x.1954 (J.H.C. and F.J.G.) ; Norseman, 5 miles NW. of, 25.x.1954 (J.H.C. and F.J.G.) ; Norseman, 8 miles NW. of, 25.x.1954 (J.H.C. and F.J.G.) ; Norseman, 20 miles NNW. of, 25.x.1954 (J.H.C. and F.J.G.) ; Salmon Gums, 2 miles S. of, 24.x.1954 (J.H.C. and F.J.G.) ; Southern Cross, 7 miles SSE. of, 30.x.1954 (J.H.C. and F.J.G.) ; 31.x.1954 (J.H.C. and F.J.G.) ; Southern Cross, 14 miles SSE. of, 30.x.1954 (J.H.C. and F.J.G.) ; Southern Cross, 2 miles WSW. of, 31.x.1954 (J.H.C. and F.J.G.) ; Southern Cross, 7 miles WSW. of, 31.x.1954 (J.H.C. and F.J.G.) ; Southern Cross, 8 miles NW. of, 30.x.1954 (J.H.C. and F.J.G.) ; Truslove, 1 mile S. of, 24.x.1954 (J.H.C. and F.J.G.) ; Widgiemooltha, 15 miles NNW. of, 26.x.1954 (J.H.C. and F.J.G.) ; Widgiemooltha, 23 miles NNW. of, 26.x.1954 (J.H.C. and F.J.G.) ; Yellowdine, 6 miles E. of, 29.x.1954 (J.H.C. and F.J.G.).

(iv) *Distribution of* C. acinaciformis (*series of soldiers and workers only*).—Albany ; Beverley ; Bridgetown ; Broome Hill ; Capel ; Collie ; Cranbrook ; Cranmore Park ; Denmark ; Dwellingup ; Ghooli ; Gnowangerup ; Goomalling ; Green Bushes ; Holyoake ; Hovea ; Jarrahdale ; Karonie ; Katanning ; Kelmscott ; Lion Mill ; Mandurah ; Manjimup ; Margaret River ; Mordo ; Mt. Barker ; Mullewa ; Mundaring ; Muradup ; Myalup ; Noggerup ; Nornalup ; Porongorups ; Quairading ; Serpentine ; Stirling Ranges ; Tammin ; Wagerup ; Wickepin ; Yarloop Mill ; (recorded by Hill 1942, under *C. acinaciformis* and *C. raffrayi*).

Abydos Hstd., 13 miles N. of, 7.vi.1953 (J.H.C.) ; Albany, 15 miles NE. of, 8.xi.1947 (T.G. and J.H.C.) ; Albany, 3 miles W. of, 7.xi.1947

(T.G. and J.H.C.) ; Armadale, 13 miles SE. of, 17.ii.1953 (J.H.C.) ; Balladonia Hstd., 20.xi.1947 (T.G. and J.H.C.) ; Balladonia Hstd., 60 miles E. of, 22.xi.1947 (T.G. and J.H.C.) ; Balladonia Hstd., 70 miles E. of, 4.x.1954 (D. H. Perry) ; Beverley, 10 miles SW. of, 27.ii.1953 (2 series) (J.H.C.) ; Bilbarin, 3 miles E. of, 3.iv.1953 (J.H.C.) ; Bilbarin, 8 miles E. of, 5.iv.1953 (J.H.C.) ; Bilbarin, 10 miles W. of, 3.iv.1953 (J.H.C.) ; Bindoon, 6 miles N. of, 11.ix.1952 (J.H.C.) ; Booanya Rock, 21.xi.1947 (T.G. and J.H.C.) ; Borden, 11 miles S. of, 9.ix.1947 (T.G. and J.H.C.) ; Bowelling, 6 miles W. of, 21.i.1953 (J.H.C.) ; Bowelling, 2 miles NW. of, 11.xi.1952 (J.H.C.) ; Boyup Brook, 4 miles WSW. of, 4.iii.1953 (J.H.C.) ; Buntine, 4 miles NNW. of, 20.iii.1953 (J.H.C.) ; Collie, 6 miles ESE. of, 11.xi.1952 (J.H.C.) ; Coolawanyah Hstd., 24 miles SSW. of, 2.vi.1953 (J.H.C.) ; Dale Bridge, 6 miles W. of, 16.i.1953 (J.H.C.) ; Dandaragan, 8 miles E. of, 17.iv.1953 (J.H.C.) ; Dardanup, 2 miles NW. of, 10.xi.1952 (J.H.C.) ; Darkan, 10 miles SE. of, 11.xi.1952 (J.H.C.) ; Debelin Rock, 26.xi.1947 (M. M. H. Wallace) ; Denmark, 1 mile W. of, 7.xi.1947 (T.G. and J.H.C.) ; Denmark, 15 miles W. of, 7.xi.1947 (T.G. and J.H.C.) ; Dwellingup, 1945 (N. Tamblyn), 19.x.1947 (4 series) (N.T.), 28.i.1948 (4 series) (A. W. Gardner) ; Galena, 18 miles NNW. of, 25.x.1953 (J.H.C.) ; Geraldton, 8 miles NE. of, 17.iii.1953 (J.H.C.) ; Gnangara Plantation, 28.vii.1954 (J.H.C.) ; Green Bushes, 3 miles NW. of, 20.i.1953 (J.H.C.) ; Holt Rock, 11 miles S. of, 3.xi.1947 (T.G. and J.H.C.) ; Hooley Hstd., 7 miles N. of, 31.v.1953 (J.H.C.) ; Huntly, 1945 (N.T.) ; Kalannie, 14 miles N. of, 28.iv.1953 (J.H.C.) ; Kalannie, 5 miles W. of, 28.iv.1953 (J.H.C.) ; Kalgoorlie, 35 miles NE. of, 31.x.1947 (T.G. and J.H.C.) ; Karragullen, 30 miles ESE. of, 27.ii.1953 (J.H.C.) ; Karratha Hstd., 4 miles W. of, 12.vi.1953 (J.H.C.) ; Katanning, 2 miles E. of, 25.xi.1947 (M.M.H.W.) ; Katanning, 12 miles E. of, 2.ii.1953 (J.H.C.) ; Katanning, 3 miles W. of, 25.xi.1947 (2 series) (M.M.H.W.) ; Kitchener, 9 miles W. of, 26.x.1947 (T.G. and J.H.C.) ; Kitchener, 10 miles W. of, 26.x.1947 (T.G. and J.H.C.) ; Kojarina, 1 mile E. of, 19.iii.1953 (J.H.C.) ; Kojonup, 2 miles NNE. of, 24.iii.1955 (J.H.C.) ; Lake Grace, 4 miles S. of, 4.xi.1947 (T.G. and J.H.C.) ; Manjimup, 16 miles SSE. of, 5.iii.1953 (J.H.C.) ; Mardie Hstd., 10 miles ENE. of, 12.vi.1953 (J.H.C.) ; Morawa, 30.x.1952 (J.H.C.) ; Morawa, 6 miles ENE. of, 15.iv.1953 (J.H.C.) ; Mt. Barker, 5 miles S. of, 6.xi.1947 (T.G. and J.H.C.) ; Mudiarrup, 9 miles WSW. of, 4.iii.1953 (J.H.C.) ; Mundiwindi, 19 miles NE. of, 24.v.1953 (J.H.C.) ; Narrogin, 7.vi.1938 (K. R. Norris) ; Neeralin Pool, 26.xi.1947 (3 series) (M.M.H.W.) ; Nornalup, 20.ii.1951 (T.G.) ; Northampton, 2 miles W. of, 18.iii.1953 (J.H.C.) ; Nungarin, 31.vii.1952 (Dept. of Works) ; Nyabing, 19.ix.1952 (J.H.C.) ; Nyabing, 14 miles N. of, 19.ix.1952 (J.H.C.) ; Ongerup, 4 miles E. of, 9.xi.1947 (T.G. and J.H.C.) ; Parkers Range, 16 miles S. of, 3.xi.1947 (2 series) (T.G. and J.H.C.) ; Parkers Range, 62 miles S. of, 3.xi.1947 (T.G. and J.H.C.) ; Parkers Range, 69 miles S. of, 3.xi.1947 (T.G. and J.H.C.) ; Paynes Find, 31 miles NNE. of, 21.v.1953

(J.H.C.) ; Pemberton, 11.xi.1927 (2 series) (A. G. Nicholls), 1945 (N.T.) ; Pingrup, 16 miles E. of, 3.ii.1953 (J.H.C.) ; Pingrup, 37 miles E. of, 3.ii.1953 (J.H.C.) ; Pingrup, 45 miles E. of, 4.ii.1953 (J.H.C.) ; Pithara, 1 mile S. of, 30.x.1952 (J.H.C.) ; Prowaka, 1 mile N. of, 16.iii.1953 (J.H.C.) ; Roy Hill Hstd., 4 miles W. of, 25.v.1953 (J.H.C.) ; Sherlock Hstd., 16 miles WNW. of, 11.vi.1953 (J.H.C.) ; Southern Cross, 7 miles SE. of, 9.viii.1952 (J.H.C.) ; Stirling Range, 8.xii.1951 (T.G.) ; Stretton, 6 miles E. of, 26.xi.1947 (M.M.H.W.) ; Whim Creek, 14 miles NNE. of, 4.vi.1953 (J.H.C.) ; Wickepin, Oct. 1947 (N.T.) ; Widgiemooltha, 6 miles N. of, 21.ix.1952 (J.H.C.) ; Woolgangie, 16 miles E. of, 2.xi.1947 (2 series) (T.G. and J.H.C.) ; Yanchep Caves, 6.ix.1951 (T.G.) ; York, 5 miles SW. of, 16.i.1953 (J.H.C.) ; York, 9 miles W. of, 16.i.1953 (J.H.C.) ; Zanthus, 5 miles W. of, 26.x.1947 (T.G. and J.H.C.).

(*c*) *Biology*

C. acinaciformis is a common and widely distributed termite species in Western Australia and is certainly the most abundant and destructive species in the southern part of the State, where practically all of the human population is concentrated. It thrives in built-up areas and is common in the Perth metropolitan district. We have collected it in regions with an annual average rainfall as low as 8 in. (Kitchener) to as high as 60 in. (Nornalup). It occurs commonly in many plant communities, dominated by *Eucalyptus* species, e.g. wet and dry sclerophyll forest, savannah woodland, mallee, and sclerophyll woodland.

The dependence of this species, and indeed all Australian *Coptotermes* species, on eucalypts is exemplified by its relative abundance on either side of the mulga-eucalypt line, a "remarkably well-defined" line in the 8-10 in. rainfall region dividing the mallee and sclerophyll woodland from the *Acacia*-dominated community of the drier interior, known as mulga bush (see Gardner 1944, pp. li-lii). *C. acinaciformis* is common in the eucalypt-dominated communities on the southern higher rainfall side of the line. North and east of the line in inland mid-Western Australia and in the north-west of the State colonies appear to be very rare and are confined to eucalypt logs and trees in the beds of water courses. The most destructive termite in this semi-arid region, a situation occupied by a species of *Coptotermes* in most settled parts of Australia, is *Schedorhinotermes intermedius actuosus* (Hill). North of the mulga-eucalypt line in the Goongarrie-Menzies region, *acinaciformis* has been found only in large mounds built in the centres of or close to occasional mallees in the mulga scrub.

The only eucalypt country where *acinaciformis* appears to be rare or even absent are areas of mallee scrub where the soil is largely deep sand where the species presumably cannot obtain clay for nest building.

C. acinaciformis attacks many species of trees of the genus *Eucalyptus* and other genera. Although no systematic survey has been carried out some observations have been gathered on the attacks of this species, mainly on eucalypts. Living trees of the following species, which appear otherwise sound, are commonly infested: salmon gum (*E. salmonophloia* F. Muell.), gimlet (*E. salubris* F. Muell.), York gum (*E. foecunda* Schau., var. *loxophleba* Benth.), karri (*E. diversicolor* F. Muell.), wandoo, Dundas mahogany (*E. brockwayi* C. A. Gardn.), a goldfields blackbutt (*E. le soeufi* Maiden), coral-flowered gum (*E. torquata* Luehm.). However, in some of these species there appears to be a considerable degree of resistance and the attack is largely confined to heartwood. Jarrah (*E. marginata* Smith) and tuart (*E. gomphocephala* A.D.C.) appear to have a high or reasonably high degree of resistance but there are a considerable number of records of attack in apparently sound trees of both species. Marri (*E. calophylla* R. Br.) and flooded gum (*E. rudis* Endl.) appear to be very resistant and the few cases of attack seen on living trees were confined to the dead sapwood of damaged trees. There is one record of attack on an apparently sound Dundas blackbutt (*E. dundasi* Maiden) which appears to be a very resistant species. River red gum (*E. camaldulensis* Dehn.), also appears to be generally resistant and only two or three instances of attack have been observed.

Our records include single or very few cases of attacks on living, apparently sound, trees of some other species but as we have examined very few trees of these species we can give no idea of their resistance to attack by *C. acinaciformis*. The species are red morrel (*E. oleosa* F. Muell. var. *longicornis* F. Muell.), mallee form of redwood (*E. oleosa* F. Muell. var. *glauca* Maiden), swamp yate (*E. occidentalis* Endl.), yorrell (*E. gracilis* F. Muell.), a dryandra (*Dryandra floribunda* R. Br.), and at least one *Banksia* species. Dead logs of the swamp sheoak (*Casuarina glauca* Sieber) and dead trees and logs of the maritime pine (*Pinus pinaster* Ait.) are frequently found being eaten by *C. acinaciformis*. Living trees of the pine are not attacked.

Living trees of all species with fire scars or other damage are attacked with much greater frequency than sound trees. Tree colonies with "blow holes" and sometimes with "white ant caps" (see Ratcliffe, Gay, and Greaves 1952, p. 78, for definitions of these terms) are commonly found with many of the above species.

In the drier parts of the range of *C. acinaciformis*, the manner in which the termites clear the forest floor of logs and sticks is very noticeable. Raised lines of soil representing the remains of the clay filling of termite-infested logs and sticks are a common sight, the wood being all or almost all consumed. *C. frenchi* is also involved in this clearing but appears to be important only in the mallee where it is commonest and the larger species is rare.

Over all of the known range, nests are found in living and dead trees, often with little or no indications on the outside of the tree, or with hard clay slabs against or around the base of the tree. These lean-to slabs can be quite large—sometimes extending 4 or 5 ft up the tree and being upwards of 2 ft thick at ground level. In sandy country where clay is scarce these slabs are sandy and somewhat more friable. Some of these colonies occupy the inside of the trunk and limbs of dead trees at least as high as 50 ft from the ground. Clay washed from checks is observed as yellow streaks on tree trunks up to this height, and we have seen alates issuing from trees up to about this height. A large living wandoo (*Eucalyptus redunca* Schauer, var. *elata* Benth.) thrown down by wind revealed infestation up to 45 ft from the ground.

In certain areas in southern Western Australia, notably east of Pingrup and a considerable distance south of the Great Eastern Highway and west of the Coolgardie-Esperance Road, this species constructs symmetrical domed mounds over tree stumps, or less commonly the mounds may have no stump or other wood inside them. Nevertheless, most colonies are found in trees with some clay workings around the base. East and north of this area mounds are found very rarely. We have not found any mounds west of Pingrup. In the area where they occur most frequently they are on clayey soil, but the presence of clayey soil is not the only requisite for their occurrence for we have seen mounds in the Goongarrie area in association with isolated patches of mallee in the mulga scrub where the soil and the mounds were quite sandy.

C. acinaciformis mounds in Western Australia may be up to 4 ft 6 in. high and about the same in diameter at the base, or perhaps a little larger. The colour varies with that of the soil and may be grey, red-brown, or most commonly some shade of yellowish brown. As is general with *Coptotermes* mounds the exterior is flaky. There is a very hard outer clay wall generally about 1 ft 6 in. although sometimes up to 2 ft or more in thickness. This is traversed by few galleries, some of those close to the surface being widened, no doubt as congregating places for the alates prior to the colonizing flight. Inside the clay wall is a spherical section about 2-2 ft 6 in. in diameter and with a thickness of only 3-6 in. which is composed of fairly loose lumps of woody honeycomb-like carton material. This hollow sphere encloses the nursery, about 2 ft or somewhat less in diameter, and composed of concentrically arranged light yellowish brown layers of fragile cardboard-like carton material. The centre of the nursery is found at about ground level or up to 1 ft or more below ground level. All sections of the mound are sharply demarcated from adjacent sections. In mounds which have no wood in their make-up usually the whole of the above-ground portion is solid clay with very few galleries, and the inner sections of the nest are all below ground level. In tree colonies the centre of the nursery may be at ground level in the root crown or 1 ft or so below ground level.

In a nest in which the queen was found, she was in a flat chamber about 4 in. from the bottom of the nursery. Eggs were found in a group of galleries all within 3 in. of the queen. Close to the eggs but in a separate group of galleries the very small nymphs were found. A mound of *C. a. raffrayi* is shown in Plate 1, Figure 1.

Symmetrical domed mounds have hitherto been recorded for this species only in parts of the Northern Territory and Queensland (Hill 1915, 1922, and 1942, p. 146). There would appear to be no evidence as yet that *C. acinaciformis* builds mound nests in tropical Western Australia, and Ratcliffe, Gay, and Greaves (1952, p. 81) are in error when they state that the name "was originally given to the mound-building form occurring in tropical Australia . . .". Froggatt's (1898) collector, W. O. Mansbridge, stated that the type series from Hall's Creek (Western Australia) was taken from the heart of an eaten-out eucalypt 20 ft from the ground, and that most of the eucalypts in the district were eaten out in the same manner. Under *C. raffrayi*, Ratcliffe, Gay, and Greaves (1952, p. 84) state that its visible nests "rarely, if ever, take the form of symmetrical domed mounds."

The mounds occurring in the Northern Territory as described by Hill (1915) differ considerably in details of construction from those of south-western Australia. The outer walls of Hill's mound were about 12 in. thick at the base but only 2 in. thick at the summit. Practically the whole of the interior consisted of lumps of honeycomb-like carton, while the nursery region was near the base of the mound forming more or less horizontal chambers. Mounds observed in the Atherton area of north Queensland (F. J. Gay, unpublished data) are basically similar to those described by Hill but the whole of the interior consisted of lumps of carton and there was no definite nursery region.

Early instar reproductice nymphs have been found in a few nests as early as the first week of February. Alates have been taken from nests in October and November. When ready to leave the nest, the alates congregate in the outer wall galleries during the daytime, particularly on the sunny side, but retreat to the inner portions of the nest at night or in cold weather. This habit has previously been reported for *C. brunneus* (Gay 1955).

Flying alates have been collected in the Perth area in all months from October 2 to January 1. However, the great mass of alates generally leaves the nests in south-western Australia in the first half of November. The colonizing flight begins any time from mid-afternoon to dusk. The numbers of alates flying reach a maximum within 15-30 min and then dwindle rapidly. However, odd ones have been taken at lights as late as 9.45 p.m. Colonizing flights generally take place on hot humid days usually a few hours or a day prior to rain. Spectacular flights of this species were observed while on a trip in south-western Australia in 1952. On November 10 and 11, flying alates were encountered in large numbers

over many miles of country in the general area of Donnybrook and Darkan. Flight began at 2.45 p.m. on November 10 and 4.20 p.m. on the following day. The numbers flying quickly reached a maximum and then decreased rapidly until by early evening there were few, if any, alates in the air. Later in the evening the numbers again increased to large proportions. Both November 10 and 11 were hot and humid and on the following afternoon and evening, this general south-western area received fairly heavy rain. It was noteworthy that on both of these days there were two distinct flying times, with maxima in mid-afternoon and evening.

III. C. MICHAELSENI

(*a*) *General and Taxonomic*

The present literature on this species contains some inaccuracies due to the fact that it has been confused with *frenchi* which until recently was thought not to occur in Western Australia, and apparently all small *Coptotermes* collected in this State were thought to be *michaelseni*. We have recently examined this question in some detail and have carried out a comparative examination of Western Australian material of these two species. Hill (1942) did not compare these species.

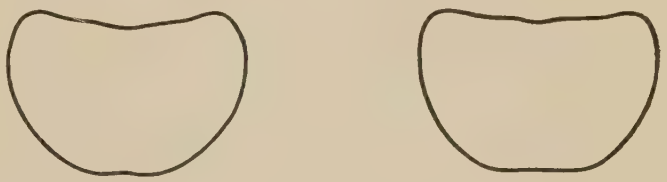

Fig. 2.—Camera lucida drawings of the pronotum of (*a*) *Coptotermes frenchi*, and (*b*) *Coptotermes michaelseni*.

The alates of the two species present no difficulty, except very occasionally with old preserved specimens, as there is a very marked colour difference, those of *michaelseni* being dark brown and *frenchi* yellowish brown. It appears that alates of *michaelseni* may occasionally fade either with time, or conditions of preservation, or some other reason. We have examined one complete series of *michaelseni*, unfortunately lacking the date of collection but known to have been collected at Perth prior to 1926, in which the alates were practically indistinguishable from *frenchi*. Professor A. E. Emerson states (personal communication) that the co-type imago of *michaelseni* in Silvestri's collection which he examined in Italy in 1926 was a medium yellow-brown and not dark brown. Not one of several hundred freshly preserved alates of *michaelseni* examined by the authors in the past few years could be described as anything but dark brown. Further, many thousands of alates have been closely observed as they emerged for the colonizing flight. On such occasions a lookout has

been kept for light-coloured alates but none have been seen. The most obvious morphological differences are in the ocelli, which are small and well separated from the eyes in *michaelseni*, whereas in *frenchi* they are conspicuously larger and frequently placed very close to the eyes, and in the shape of the pronotum which is always more obviously concave anteriorly and narrow posteriorly in *frenchi* (see Fig. 2).

The soldiers are very similar but can be separated by combinations of certain head measurements. Table 1 gives a series of measurements of a number of soldiers of Western Australian *michaelseni* and *frenchi* known to be correctly identified by their associated alates. Measurements of some series containing soldiers and workers only, gave minima somewhat below those of soldiers from complete series. These are included in the table in brackets to give a more complete idea of the size range of the species.

The measurements of the soldiers of the two species are very similar in almost all cases but there are two or three dimensions that are generally significantly different and these can be grouped to give a clear separation of the two species. The maximum head width in *frenchi* is rarely under 1.00 mm whereas in *michaelseni* it never attains this size. Since the minimum head width is about the same in both species it follows that *michaelseni* has an almost straight-sided, evenly-tapered head whilst in *frenchi* it is obviously swollen at the sides. This point is clear from Hill's excellent figures. The left mandible is generally somewhat longer in *frenchi* than in *michaelseni* and one gets a definite impression that the mandibles are longer and stouter in the former species. The gula measurements although overlapping show that the minimum width in *frenchi* is generally greater than in *michaelseni*. Antennal segments although commonly 14 for both species show instances of 15 in *frenchi* and 13 or 15 in *michaelseni*.

Two series, containing soldiers and workers only, have not been included in the foregoing discussion. One of these is a series of *michaelseni* (Fremantle, 19.vii.1938) containing both normal and nanitic soldiers. In the other series (Coolgardie, 27 miles WSW. of, 6.xii.1953) the maximum measurements for head length and width of the soldiers is equal to or below the minimum for *michaelseni*, but the figures for length of left mandible and minimum gula width are towards the upper limit for *michaelseni*. It is concluded that this is a nanitic series of *frenchi*, the conclusion being supported by the fact that the series was collected from a very small, presumably young, colony.

Some of the series of soldiers recorded by Hill (1942) as *michaelseni* have been re-examined and are now considered to have been misidentified *frenchi*. Strangely enough four of these series have been labelled by Hill "compared with co-type." Ten soldiers from each of three of these series and seven from the fourth were measured, and the variation in maximum head width was found to be 1.00-1.07 mm. Other measurements and

TABLE 1

RANGE OF MEASUREMENTS OF SOLDIERS OF WESTERN AUSTRALIAN SPECIMENS OF COPTOTERMES FRENCHI AND C. MICHAELSENI KNOWN TO BE CORRECTLY IDENTIFIED BY THEIR ASSOCIATED ALATES

The figures in brackets, included for completeness, are lower minima obtained from series of soldiers and workers only

Measurement	*C. frenchi*	*C. michaelseni*
Number measured:		
From complete series	58	70
From series containing soldiers and workers only	32	61
Head and mandibles, long	1.87-2.12 mm	(1.67) 1.79-2.07 mm
Head without mandibles, long	(1.21) 1.26-1.39 mm	(1.15) 1.23-1.35 mm
Head to fontanelle, long	(1.13) 1.17-1.30 mm	(1.10) 1.12-1.28 mm
Head, maximum width	0.96-1.10 mm	(0.84) 0.93-0.99 mm
Head, minimum width	0.55-0.62 mm	(0.51) 0.55-0.62 mm
Left mandible, long	0.71-0.82 mm	(0.53) 0.66-0.73 mm
Pronotum, wide	0.73-0.84 mm	(0.64) 0.73-0.82 mm
Pronotum, long	(0.38) 0.39-0.46 mm	(0.34) 0.38-0.45 mm
Gula, minimum width	0.25-0.31 mm	(0.21) 0.23-0.28 mm
Antennae, segments	14-15	(13) 14-15

Collecting data for series measured

Complete series	Pingrup, 36 miles E. of, 31.x.53 Pingrup, 29 miles E. of, 31.x.53 Pingrup, 16 miles E. of, 1.xi.53 Nyabing, 7 miles N. of, 31.x.53 Nyabing, 11 miles WSW. of, 30.x.53 Borden, 11 miles S. of, 9.xi.47 Badjaling, 3 miles SE. of, 26.xi. 47	Perth (Subiaco), 5.ix.51 Perth (Nedlands) (2 different series) 10.ix.53 and 8.xi.53 Safety Bay, 5 miles ESE. of, (2 different series) 13.viii.54
Series containing soldiers and workers only	Gnowangerup, 6.iii.28 Gnowangerup, 15 miles N. of, 26.iv.41 Kuringup, 26.iv.41 Kuringup Siding, 26.iv.41 Lake Grace, 26.iv.41	Albany Rd., 70 miles S. of Perth, 27.iv.41 Perth (South Perth) (3 different series) 5.v.41 Perth (Karrakatta) (Hamburg S.W. Australia Exped. 1905; in W.A. Mus.) Beverley, 16 miles S.W. of, 11.viii.54 Bullsbrook, 10 miles N. of, 25.viii.54

the general appearance of the soldiers supported our identification. As Hill gave 0.99 mm as the maximum head width for *michaelseni* (i.e. the

same as our figure) it would appear that he made his comparisons by eye only. Two of these series are from Gnowangerup and Kuringup respectively and are important in that they were taken from mounds and are two of the series, possibly the only two, on which the alleged mound-building habit of *michaelseni* was based.

It was thought possible that the "co-types" of *michaelseni* may have been misidentified and the series in the Western Australian Museum said to comprise co-types (Hill 1942, p. 164) was examined. It was found that the W.A. Museum series, the only series of this species received from the Michaelsen-Hartmeyer expedition are not co-types and are not designated as such either on the labels or in the museum register. As it is labelled "Karrakatta", and as Silvestri (1909) indicated that his series from Mundijong was the "exempla typica descriptionis", it follows that the Karrakatta specimens could not be co-types. However, the fact that these specimens were before Silvestri when he described the species gives them some taxonomic value. The series, consisting of three soldiers and six workers proved on examination to be definitely referable to *michaelseni.* Hill's co-type series of *michaelseni* is now in the custody of Professor A. E. Emerson. It consists of one soldier and two workers and the label in Silvestri's handwriting includes "cotypi" (Prof. Emerson, personal communication).

In view of this confusion Hill's records of *michaelseni* cannot be accepted without re-examination of his collections. From an examination of Silvestri's (1909) description and figures it is concluded that the species described is the same as what the authors now consider to be *michaelseni.* Mjöberg (1920) has recorded *michaelseni* from South Australia and Queensland. As *frenchi* was not described until 1926 (under the name of *C. flavus,* subsequently found to be pre-occupied) and as pointed out by Hill (1942, p. 164) Mjöberg's definition of *michaelseni* would include *frenchi,* Mjöberg's records are therefore to be discredited. Professor Emerson (personal communication) has redetermined as *frenchi* a series of soldiers and workers in his collection which was originally labelled "C. michaelseni det. coll. E. Mjöberg. Adelaide, S. Australia." Mjöberg also misidentified specimens of other *Coptotermes* species (Hill 1942, p. 162).

Hill doubtfully recorded soldiers of *michaelseni* from various localities in South Australia and Victoria and stated that they "agree(d) with co-types and other series from Western Australia". We have examined and measured series so identified by him from Cohuna (Vic.) and Narracoorte and Echunga (S.A.) and they are definitely *frenchi.* Hill's extra-Western Australian records of *michaelseni* should therefore be deleted.

In spite of the close similarity of these two species and the difficulty of separating them in the soldier caste, which, however, is not unusual with *Coptotermes* species, and also in spite of the fact that we have not yet

established any overlap in distribution, the authors believe that they are good species.

The known distribution of *C. michaelseni* is shown on Figure 3.

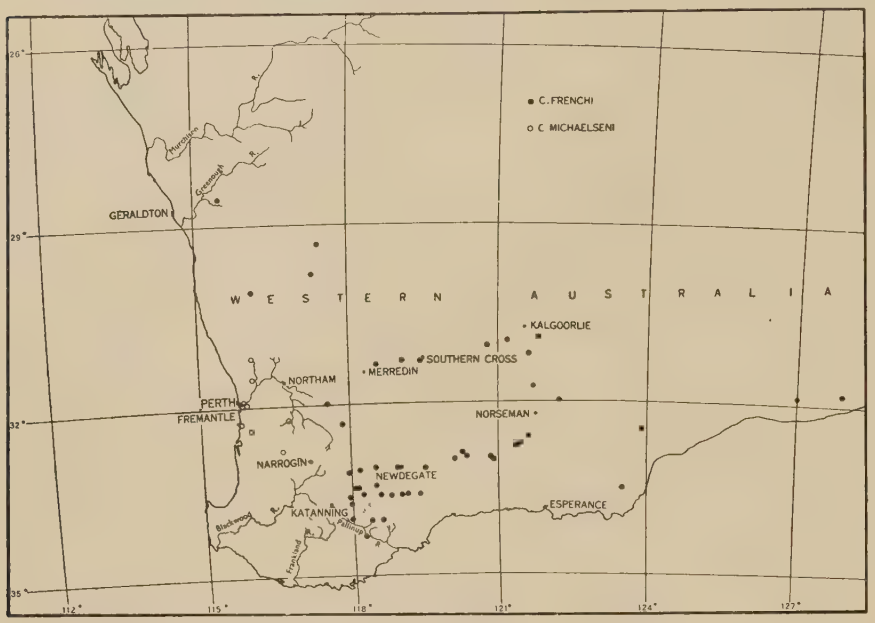

Fig. 3.—Map showing known total distribution of *C. michaelseni* (○) and known distribution in Western Australia of *C. frenchi* (●).

(*b*) *Distribution Records*

(i) *Alates or Complete Nest Series.*—Mundijong; (from Silvestri 1909).

Bindoon, 6 miles N. of, 28.viii.1953 (J.H.C.); Perth (city and Nedlands), 3-14.ix.1953 (J.H.C.); Perth (Kings Park), 26.viii.1954 (J.H.C.), 27.viii.1954 (J.H.C.); Perth (Nedlands), 21.viii.1953 (J.H.C.), 10.ix.1953 (A. R. Main), 25.ix.1953 (J.H.C.), 8.xi.1953 (J.H.C.), 8.xi.1953 (A. R. and B. Y. Main), 27.viii.1954 (J.H.C.), 28.viii.1954 (J.H.C.), 7.ix.1954 (J.H.C.), 14.ix.1954 (J.H.C.), 19.ix.1954 (J.H.C.), 1.x.1954 (J.H.C.), 2.x.1954 (J.H.C.), 10.x.1954 (J.H.C.); Perth (Subiaco), 5.ix.1951 (T.G.); Safety Bay, 5 miles ESE. of, 13.viii.1954 (2 series) (J.H.C.).

(ii) *Series of Soldiers and Workers Only.*—Perth (Guildford); Perth (Karrakatta); Perth (Subiaco); (from Silvestri 1909).

Albany Rd., 70 miles S. of Perth, 27.iv.1941 (F. N. Ratcliffe); Beverley, 16 miles SW. of, 11.viii.1954 (J.H.C.); Bullsbrook, 10 miles N. of, 25.viii.1954 (J.H.C.); Fremantle, 19.vii.1938 (M. F. Day); Gnangara Plantation, 28.vii.1954 (J.H.C.); Keysbrook, 1 mile N. of, 10.xi.1952 (J.H.C.); Perth (Applecross), 14.xii.1951 (P. Sturtridge); Perth (South

Perth), 5.v.1941 (3 series) (F.N.R.); Sawyers Valley, 2 miles E. of, 5.iv.1955 (J.H.C.).

(*c*) *Biology*

Hill (1942, p. 164) and Ratcliffe, Gay, and Greaves (1952, p. 85) state that *michaelseni* is a mound builder. These are the only authors who give this information, the source being the same in both cases. Recent evidence and observations, however, indicate that *michaelseni* is not a mound builder, the error having arisen from the confusion of soldiers of this species with soldiers of *frenchi* as explained above.

Very little can be said about the habits of *michaelseni* and, as yet, the nursery region of any nests has not been found. It apparently builds subterranean nests. Soldiers and workers are commonly found under small logs and other pieces of wood and litter in contact with the ground, and often in mud-covered runways up the sides of dead wood and structural timber. One of the timbers eaten by this species is jarrah which appears to be sound. Like *acinaciformis* it eats dead trees and sticks of the maritime pine but does not attack living trees. The centres of posts and logs are sometimes found eaten out by *michaelseni* and filled with lumpy or damp, fairly solid, clayey material. The species is very common in the Perth area judging by the number of alates flying in early spring.

Alates have been found under and in dead sticks and small logs in contact with the ground, in August, and have been collected flying between August 21 and November 8. They appear in large numbers in the third or fourth week of August and are seen fairly frequently for the next few weeks. Colonizing flights take place during the warmer parts of warm, sunny, generally cloudless and fairly still days. We have records of the beginning of the colonizing flight on different days in the Perth area from as early as 11.15 a.m. to as late as 4.20 p.m., but most commonly flight begins in the early afternoon. Our records show that flying has ceased by sunset or shortly after. As with *acinaciformis* the numbers flying quickly reach a maximum and then dwindle rapidly. We have one record of two flight peaks in one day. Flying began at 11.15 a.m. and lasted until 5.00 p.m., with very definite peaks at 11.30 a.m. and 2.15 p.m.

Alates have been observed on many occasions issuing from holes or slits in the ground. They emerged quickly in a constant stream and usually climbed up grass stalks and herbage before launching. Many soldiers and a few workers walked about on the ground around the holes and the mandibles and waving antennae of many other soldiers projected from the holes.

IV. C. FRENCHI

(*a*) *General*

C. frenchi is here recorded for the first time as occurring in Western Australia. As explained under the preceding species, Hill had examined soldiers of *frenchi* from Western Australia but misidentified them as

michaelseni. Ratcliffe, Gay, and Greaves (1952, p. 79) recorded the presence in this state of specimens taken from mounds which were morphologically similar to *frenchi,* but reserved judgment on their final identification because the mound-nesting habit was quite unlike the tree-nesting habits of typical *frenchi* from south-eastern Australia.

There is no good reason why these specimens should not be referred to *frenchi,* as another Australian species of *Coptotermes,* viz. *acinaciformis* builds symmetrical domed mounds in a part only of its total range. Morphologically, the mound-building form, which also occurs in parts of semi-arid South Australia, is indistinguishable from the typical form of eastern Australia. The known distribution of *C. frenchi* in Western Australia is shown in Figure 3.

(*b*) *Distribution Records*

(i) *Alates or Complete Nest Series.*—Badjaling, 3 miles SE. of, 26.xi.1947 (M.M.H.W.) ; Borden, 11 miles S. of, 9.xi.1947 (T.G. and J.H.C.) ; Bulla Bulling, 9 miles WSW. of, 29.x.1954 (J.H.C. and F.J.G.) ; Daniell, 15 miles SW. of, 23.x.1954 (J.H.C. and F.J.G.) ; Daniell, 21 miles SW. of, 23.x.1954 (J.H.C. and F.J.G.) ; Higginsville, 2 miles SW. of, 25.x.1954 (J.H.C. and F.J.G.) ; Kukerin, 4 miles NE. of, 20.x.1954 (J.H.C. and F.J.G.) ; Kukerin, 8 miles W. of, 20.x.1954 (J.H.C. and F.J.G.) ; Lake King, 32 miles ENE. of, 22.x.1954 (J.H.C. and F.J.G.) ; Mt. Ragged, 18.xi.1947 (T.G. and J.H.C.), 14.xii.1953 (J.H.C.) ; Mundrabilla Hstd., 23.xi.1947 (T.G. and J.H.C.) ; 90-Mile Tank, 27 miles ESE. of, 23.x.1954 (J.H.C. and F.J.G.) ; 90-Mile Tank, 11 miles SW. of, 22.x.1954 (J.H.C. and F.J.G.) ; 90-Mile Tank, 13 miles SW. of, 22.x.1954 (J.H.C. and F.J.G.) ; Nyabing, 7 miles N. of, 30.x.1953 (J.H.C.) ; Nyabing, 11 miles WSW. of, 30.x.1953 (J.H.C.) ; Ongerup, 4 miles E. of, 9.xi.1947 (T.G. and J.H.C.) ; Pingrup, 16 miles E. of, 1.xi.1953 (J.H.C.) ; Pingrup, 29 miles E. of, 31.x.1953 (J.H.C.) ; Pingrup, 36 miles E. of, 31.x.1953 (J.H.C.) ; Ravensthorp, 2 miles W. of, 10.xi.1947 (T.G. and J.H.C.).

(ii) *Series of Soldiers and Workers Only.*—Balladonia Hstd., 20.xi.1947 (T.G. and J.H.C.) ; Burracoppin, 2 miles ENE. of, 31.x.1954 (J.H.C. and F.J.G.) ; Coolgardie, 27 miles WSW. of, 6.xii.1953 (J.H.C.) ; Coolgardie, 2 miles W. of, 22.ix.1952 (J.H.C.) ; Corrigin, 3.iv.1953 (J.H.C.) ; Daniell, 20.ix.1952 (J.H.C.) ; Darkan, 10 miles SE. of, 22.i.1953 (J.H.C.) ; Gnowangerup, 6.iii.1928 (A.G.N.) ; Gnowangerup, 15 miles N. of, 26.iv.1941 (F.N.R.) ; Kuringup, 26.iv.1941 (F.N.R.) ; Kuringup Siding, 26.iv.1941 (F.N.R.) ; Lake Grace, 24.iv.1941 (F.N.R.) ; Lake King, 40 miles ENE. of, 20.ix.1952 (J.H.C.) ; Madura Hstd., 5.x.1954 (D. H. Perry) ; Moorine Rock, 4 miles W. of, 23.ix.1952 (J.H.C.) ; Mullewa, 6 miles SW. of, 20.viii.1953 (J.H.C.) ; Newdegate, 24 miles E. of, 4.xi.1947 (T.G. and J.H.C.) ; Newdegate, 6 miles W. of, 4.xi.1947 (T.G. and J.H.C.) ; 90-Mile Tank, 23 miles ESE. of, 23.x.1954 (J.H.C. and F.J.G.) ; Norseman, 29 miles

ENE. of, 8.xii.1953 (J.H.C.) ; Nyabing, 8 miles NNW. of, 2.ii.1953 (J.H.C.) ; Ongerup, 2 miles W. of, 4.xi.1947 (T.G. and J.H.C.) ; Pingrup, 11 miles N. of, 4.xi.1947 (T.G. and J.H.C.) ; Pingrup, 5 miles E. of, 3.ii.1953 (J.H.C.) ; Pingrup, 30 miles E. of, 5.ii.1953 (J.H.C.) ; Pingrup, 45 miles E. of, 4.ii.1953 (J.H.C.) ; Paynes Find, 20 miles W. of, 21.v.1953 (J.H.C.) ; Randells, 26 miles W. of, 27.x.1947 (T.G. and J.H.C.) ; Southern Cross, 7 miles SE. of, 9.viii.1952 (J.H.C.) ; Watheroo, 13 miles N. of, 27.x.1952 (J.H.C.) ; Widgiemooltha, 20 miles N. of, 8.viii.1952 (J.H.C.) ; Wubin, 43 miles NE. of, 20.v.1953 (J.H.C.).

It might serve a useful purpose to add here, records of *C. frenchi* taken from mounds in South Australia.

SOUTH AUSTRALIA: *Alates or Complete Nest Series.*—Colona, 15 miles SE. of, 25.xi.1947 (T.G. and J.H.C.) ; Immarna, 4 miles W. of, 19.x.1947 (T.G. and J.H.C.) ; Malbooma, 1 mile E. of, 16.x.1947 (T.G. and J.H.C.) ; Malbooma, 8 miles E. of, 16.x.1947 (T.G. and J.H.C.) ; Penong, 50 miles W. of, 26.xi.1947 (T.G. and J.H.C.) ; Port Augusta, 41 miles NW. of, 14.x.1947 (T.G. and J.H.C.) ; Woocalla, 31 miles SE. of, 14.x.1947 (T.G. and J.H.C.).

SOUTH AUSTRALIA: *Series of Soldiers Only.*—Yunta (from Hill, 1942, who gave this as a doubtful record only because of the supposedly anomalous mound-building habit) ; Wynbring, 15 miles W. of, 17.x.1947 (T.G. and J.H.C.).

(*c*) *Biology*

There is no information on the economic status of *frenchi* in Western Australia or whether it forms nests in living trees as it does in south-eastern Australia. It is usually found eating small dead logs and sticks in contact with the ground. Its habit of cleaning up wood litter on the forest floor has already been mentioned under *C. acinaciformis.* There are a few records of it eating living trees, all of them mallees of *E. oleosa* var. *glauca.* The insects had eaten out the centres of mallees or were in galleries in the heartwood and there was no external evidence of their presence. No instances are known of this species and *acinaciformis* occupying the same piece of wood.

In the mallee and sclerophyll woodland in the central southern part of the State where this species is common, it is generally found in symmetrical domed mounds. These mounds are usually built on clear ground quite often close to certain mallee species which grow on clayey soil. Mounds are also found in the centres of mallees, with branches protruding through them. They are common in the same general area as are mounds of *acinaciformis.* It seems probable that colonies of the two species are generally established on different soil types as their nests in this region are usually associated with different plant associations, e.g. *frenchi* is often found with mallees (*E. oleosa* var. *glauca* and *E. calycogona* Turcz.) and *acinaciformis* is found in stands of *E. salmonophloia.*

The mounds vary in colour with the soil but are usually some shade of yellowish brown. The exterior surface is very flaky. The maximum size is about 2 ft high and 4 ft in diameter at the base, although most mounds are smaller than this, and the most usual size is about 1 ft high and 1 ft 6 in. in diameter. The thicknesses of the component parts of the mound vary somewhat with the size of the mound. The outer wall is about 3 in. thick in an average mound and up to 8 in. thick in large mounds. The number of galleries through the outer wall appears to vary with individual mounds and generally there are comparatively few, although in some mounds the outer wall appears fairly cellular particularly near the inner edge. Near the outer edge there are a few broad flat galleries particularly on the upper part which often appears quite spongy. In these galleries the alates congregate during the warm part of the day, and, as in other species, retreat to the inner parts of the nest in the evening. The outer wall structure extends out into the soil for a few inches around the mound.

The middle section of the mound is roughly spherical and in an average mound is about 2 ft in diameter and has a wall thickness of about 7 or 8 in. It is solid, hard, and woody, quite unlike the relatively loose honeycomb material in the mounds of other *Coptotermes* species. This central portion is traversed by a complex network of galleries. Inside the central portion is the nursery which in an average mound is about 9 in. in diameter. It is similar to the nursery in other *Coptotermes* nests, being composed of concentric layers of thin fragile cardboard-like material. All sections of the mound are sharply demarcated from adjacent sections.

In nests examined in detail the eggs and very small nymphs were concentrated in separate groups of cells close to one another in the nursery region or in broad flat cells in the woody central portion below or on the side of the nursery. In one nest the queen was found in a broad flat cell in the woody central portion on the side, towards the bottom of the nursery. The queen was close to but separated from the eggs and tiny nymphs. Plate 1, Figure 2, is a photograph of a typical mound of *C. frenchi*.

Early instar reproductive nymphs have been found in Western Australia in a few mounds in early February and alates have been collected from mounds in October and November. Alates have been taken on the wing on one occasion only, in December, when they were attracted to a light and were flying from 6.45 to 7.20 p.m.

V. C. BRUNNEUS

All the information available to date on this recently discovered species is given in the original description (Gay 1955). The known, very restricted distribution, north of the Murchison River, is shown in Figure 1. The large size and very dark head colour distinguish the soldier from all other Australian members of the genus. The alate is also the darkest of the

WESTERN AUSTRALIAN COPTOTERMES

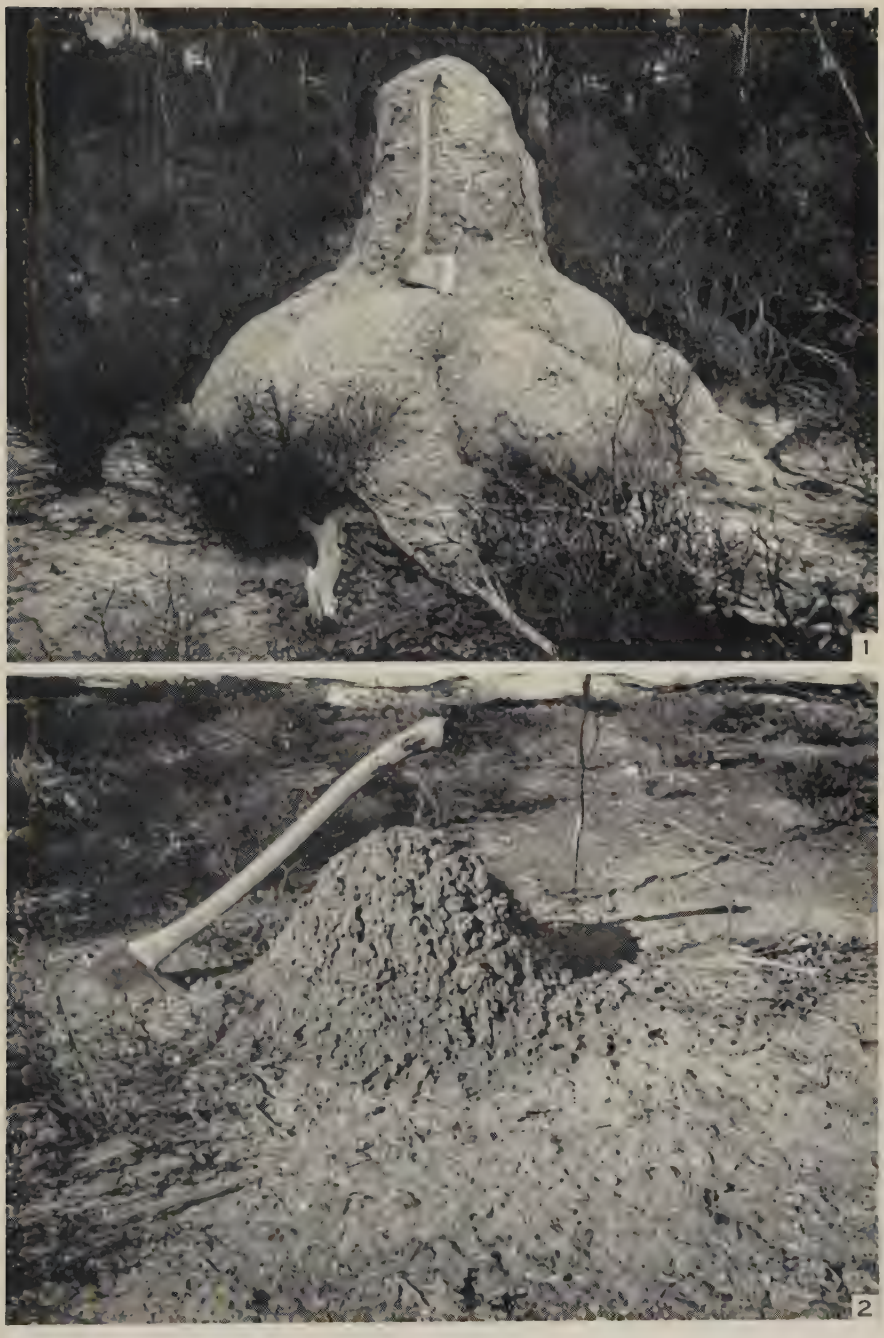

Fig. 1.—Mound of *C. a. raffrayi*, 37 miles east of Pingrup, W.A. (Photograph by J. H. Calaby.)

Fig. 2.—Mound of *C. frenchi*, 31 miles east of Pingrup, W.A. (Photograph by J. H. Calaby.)

WESTERN AUSTRALIAN COPTOTERMES

Mound of *C. brunneus* from which the type specimens were taken, 51 miles north-north-east of Galena, W.A. (Photograph by J. H. Calaby.)

Australian species and can be separated from other dark species on a number of characters.

C. brunneus inhabits sclerophyllous woodland and mallee scrub and builds large symmetrical domed to conical mounds which may be 8 ft high and 5 ft in diameter at the base. The mound is almost entirely a mass of clay with few galleries. Almost all of the nest proper is underground and consists of a large mass of loose lumps of carton. Alates ready for dispersal were found in the nests in October and it is assumed that colonizing flights take place at the same time of year as those of *C. acinaciformis*. Plate 2 is a photograph of the mound from which the type specimens were taken.

VI. Acknowledgments

The authors are indebted to Mr. C. A. Gardner, Government Botanist, Western Australia, for identifying specimens of some of the less familiar eucalypts; to the authorities of the Western Australian Museum for permission to examine the supposed co-types of *C. michaelseni*; to Miss B. J. Gemmell and Mrs. B. V. Perry for the preparation of the distribution maps; and to Mr. D. L. McIntosh for technical assistance in the field.

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STUDIES IN FUNCTIONAL AND ANALYTICAL CRANIOLOGY

XI. EXPERIMENTS WITH THE DECALCIFIED SKULL OF THE DOG

By R. TUCKER*

(*Manuscript received July* 19, 1955)

Summary

Experiments were carried out on the decalcified skull of a dog in order to estimate experimentally the location of stresses in the breviarcuate skull. The results reached are in agreement with the main functional conclusions of the previous studies (Tucker 1954*a-f*, 1955*a-d*). However, new information has been obtained about the mechanical conditions in the glenoid cavity and the topography of the areas influenced by the temporal and masseter muscles.

I. INTRODUCTION

The material gathered and investigated in previous studies (Tucker 1954*a-f*, 1955*a-d*) appeared very difficult for the initial experimental analysis. However, to check experimentally the main roots of the masticatory stresses the following experiments were devised.

II. MATERIALS AND METHODS

The skull of a dog was decalcified using 5 per cent. nitric acid, and after decalcification it was kept moist. The soft and elastic structure resulting retains its normal shape, but has the advantage of undergoing an elastic deformation when subjected to comparatively small forces, clearly indicating the position of the stresses in question.

The experiments were carried out in two series: firstly, forces were applied to the cranium directly; secondly, forces were applied by means of the mandible. The test with directly applied forces was made with two variants (i) with the skull fixed at the level of the foramen occipitale magnum and carnassial to avoid anterior or posterior shifting of parts of the skull, and (ii) without this support. Thus three skulls of small dogs were used for all described observations.

III. REACTIONS OF THE DECALCIFIED SKULL TO FORCES APPLIED DIRECTLY TO THE CRANIUM

The decalcified skull was placed on a wax block, and two scalpel blades placed at the level of carnassial and foramen occipitale magnum kept the skull in position. The blades were fixed by embedding in the wax block.

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(*a*) *Experiment* 1

Force was applied at both zygomatic arches simultaneously (Figs. 1*A* and 2(*1*)) by pressing the arches slightly downwards with the fingers. In living animals, the contraction of the masseters would exercise a force

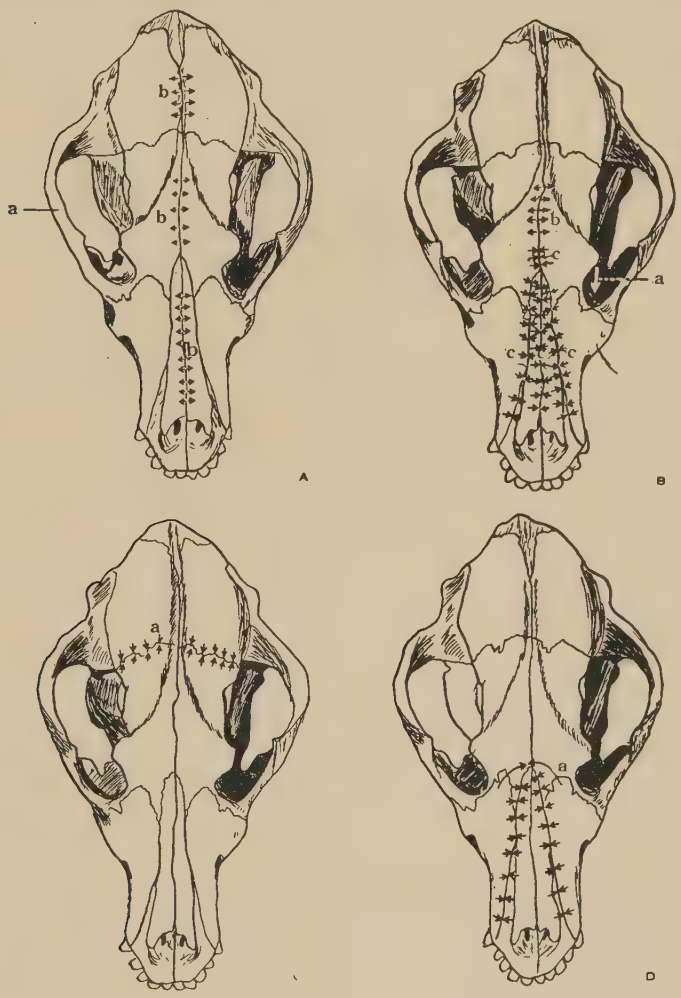


Fig. 1*A-D.*—Dorsal view of the dog's skull. *A*: *a*, Position of force applied in experiment 1; *b*, location of laterally directed stresses. *B*: Topography of compressions resulting from forces applied at the postorbital processes. *a*, Position of force applied and its direction; *b*, location of compressions; *c*, location of laterally directed stresses. *C*: Arrows indicate direction of stresses. *a*, Fronto-parietal suture. *D*: *a*, Direction of translocation of the frontal process of the maxilla.

having the same location and duration. It resulted in widening of the internasal, interfrontal, and interparietal sutures. Apparently the stresses at the roof of the skull are directed laterally (Figs. 1*A* and 2(*1*)).

(*b*) *Experiment* 2

Force was applied at the postorbital processes by means of finger pressure directed antero-ventrally (Figs. 1*B* and 2(*2*) ; Plate 1, Fig. 9(*2*)). The stresses evoked in this way correspond to the forces transmitted from the zygomatic arch, during contraction of the masseter, onto the postorbital process of the frontal bone by means of the postorbital ligament. The direction of forces transmitted by the postorbital ligament is roughly from dorsal to ventral.

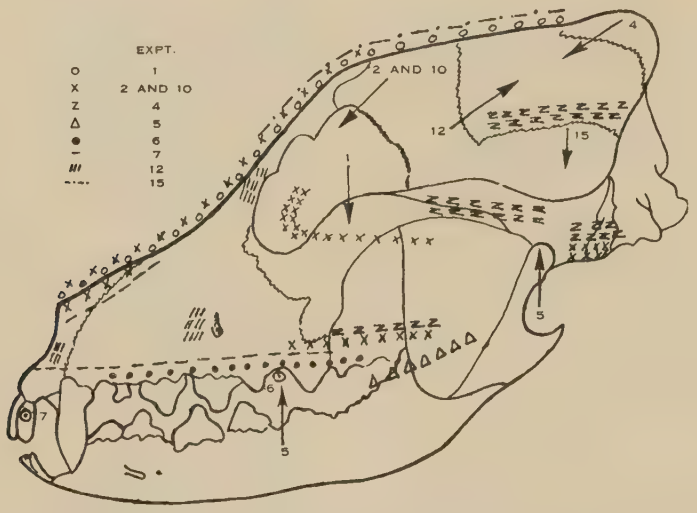


Fig. 2.—Location of forces applied during experiments 1-15 (indicated by numbers), and the topography of detectable stresses induced by them in the breviarcuate skull. Arrows indicate the direction of application of the forces. Symbols corresponding to these numbers (see legend) indicate the parts reacting.

The effects on the roof of the skull of stresses directed strictly ventrally can be easily deduced from experiment 1, while any force applied on the postorbital process directed ventrally and posteriorly (if the possibility of the existence of such forces were considered) will simply result in the substitution of the tensions for pressures and pressures for tensions in the results described below.

As an effect of the forces applied at the postorbital process and directed anteriorly and ventrally, the internasal, interfrontal (in its anterior part), and naso-maxillary sutures (the latter especially in its posterior part) were compressed (Figs. 1*B* and 2(*2*) ; Plate 1, Fig. 9(*2*)), the lower part of the frontal bone (within the orbit) was translocated medially, and the fronto-lacrimal suture was disjointed. The maxillo-squamosal tract moved downwards, and the connections between the palatine and sphenoid bones became loose. Plate 1, Figure 1, shows the topography of the abovementioned translocations in the lateral wall of the skull.

(*c*) *Experiment* 3

Force was applied at the postorbital processes, directed slightly antero-ventrally, and exerted in the same way as in experiment 2, but the skull was not fixed by the scalpel blades behind the occipital bone and at the maxillary node. The deformations at the roof of the skull were similar to those of experiment 2. The compressions at the level of the frontal process of the maxilla were visible, as well as the disjunction of the lacrimo-frontal and fronto-maxillary sutures. The maxillo-squamosal tract was displaced to a lower level than in experiment 2. The changes in the maxillo-squamosal tract and especially the connections of the basioccipital were of similar type to those in experiment 2, and the maxillary and squamosal nodes were parted more than in that experiment.

(*d*) *Experiment* 4

Forces, directed anteriorly and ventrally and representing the main axis of action of the temporal muscle, were applied directly to both parietal bones (Plate 1, Figs. 2*a* and 9(*4*) ; Fig. 2(*4*)). The exact representation of the action of the temporal muscle with finger pressure is difficult since the artificially applied force has, in addition, an internally directed component (pressure towards the cranial cavity) while the temporal muscle has an externally directed component (causing the tendency towards the lateral translocation of the parietal bone). More exact imitation of the natural conditions would be obtained by gluing elastic bands to the surface of the parietal bones, and exerting the force by pulling them. However, another difficulty arises here, namely the gluing onto a wet surface, which is necessary since the dried skull is not capable of elastic transformations.

On the other hand, the force applied by means of finger pressure is able to reproduce the more important antero-ventral vector which also originates from the contractions of the temporal muscle. Accordingly, the experiment was designed to detect the effects of these stresses on the cranial structure.

Thus these forces applied to both parietal bones resulted in a small anterior translocation of the zygomatic arch, a compression at the level of the palatine bone, and the disjunction of the squamoso-parietal connections.

(*e*) *Experiment* 5

Forces were applied in the dorsal direction by means of finger pressure at the level of the maxillary and squamosal bones (Plate 1, Figs. 3 and 9(*5*) ; Fig. 2(*5*)). This test was designed to investigate the effect of stresses which act simultaneously in the regions of the maxillary and squamosal nodes, and which correspond to the secondary stresses which appear in these nodes during mastication (Tucker 1954*a*). The sutures between the pre-sphenoid and more anterior parts widened (Plate 1, Fig. 3). However, the fronto-parietal suture (Fig. 1*C*) was markedly compressed, thus illustrating the strains along the sagittal crest.

(*f*) *Experiment* 6

Forces were applied by means of finger pressure at the level of the carnassials and directed laterally (Plate 1, Fig. 4 (arrows on carnassials); Fig. 2(*6*)) to imitate the transverse stresses developed between the upper and lower rows of dentition. The interpalatine and intermaxillary sutures widened (Plate 1, Fig. 4*a*, *b*).

(*g*) *Experiment* 7

Forces were applied by means of finger pressure at the premaxillary node (ventral approach) (Plate 1, Figs. 5 and 9(*7*); Fig. 2(*7*)). These dorsally directed forces correspond to the forces acting on the incisors during mastication. They resulted in the disjunction of the premaxillo-maxillary suture (Plate 1, Fig. 5), and the opening of sutures in the maxillo-squamosal tract.

IV. Reactions of the Decalcified Skull to Stresses Transmitted through the Mandible

The skull used for these experiments was decalcified in the way described previously, but the mandible used was not decalcified. The left half of the mandible was mounted on a wax block and the decalcified skull placed on it.

(*a*) *Experiment* 8

A ventrally directed force was applied by pressing downwards on the left zygomatic arch. The skull was supported on the opposite side to keep it in the normal position throughout the experiment. This experiment was designed to find what stresses arise in one antimere of the skull (the left in this experiment) under the force of the masseter on the corresponding side. It was observed that the changes in the internasal, interfrontal, and interparietal sutures were similar to those of experiment 1, namely the widening of the sutures (Fig. 1*A*). The glenoid cavity became translocated medially. The carnassials and molars showed deep impressions which resulted from stresses in the maxillary node. The intermaxillary suture widened, and the splanchnocranium moved upwards slightly. This experiment revealed the transverse stresses in the base of the skull during the action of the masseter. These stresses, as illustrated by the median translocation of the glenoid cavity, will be discussed later.

(*b*) *Experiment* 9

This experiment was designed to find the forces which resist the median translocation of the glenoid cavity with regard to the articular process of the mandible. A ventrally directed force was applied by means of finger pressure at both zygomatic arches. Most changes observed were similar to those obtained in experiment 8. However, the glenoid cavity remained on the articular process of the mandible. The resisting force was found to be supplied by the masseter on the opposite side of the skull.

(*c*) *Experiment* 10

A ventrally directed force was applied by means of finger pressure at the postorbital process (Plate 1, Fig. 9(*10*); Fig. 2(*10*)). As a result, the maxillary node pressed deeply into the mandibular molars. The fronto-maxillary and lacrimo-maxillary sutures were displaced. Marked disjunction was also demonstrated along the spheno-palatine and palato-frontal connections. The squamosal node was translocated caudally, resulting in the posterior translocation of the glenoid cavity relative to the articular process of the mandible (Plate 1, Fig. 6). This experiment was designed to find the effects originating from the vertical vector of the masseter during the contractions of this muscle. This vector thus gives rise to the saggital tensions in the maxillo-squamosal tract. The analysis of these stresses was discussed at length in Part III of this series (Tucker 1954*c*). The displacement of the glenoid cavity is new evidence of the existence of these stresses.

(*d*) *Experiment* 11

Forces were applied by means of finger pressure at the level of the parietal bones and directed anteriorly and ventrally (all the remarks about the difficulties in the application of the force in connection with expt. 4 are true also for expt. 11). As a result, anteriorly directed stresses were demonstrated in the premaxillary and maxillary nodes. The glenoid cavity was translocated anteriorly, and in consequence of this, the spheno-zygomatic curvature pressed against the coronoid (temporal) process of the mandible. The experiment resulted in the finding of opposing stresses for the stresses originating from the vertical vector of the masseter (see expt. 10) at the level of glenoid cavity. The opposing stresses are supplied by the temporal muscle.

(*e*) *Experiment* 12

In this and subsequent experiments the mandible was freed from the wax block. It was articulated with the skull and moved freely.

Force was applied by means of finger pressure to the coronoid process of the mandible on one side, and directed dorsally and posteriorly (Fig. 2(*12*)), to represent the main action of the temporal muscle on the mandible. It resulted in well-marked rotative tendencies at the premaxillary and maxillary bones. The inter-premaxillary suture was disjointed and the left premaxilla and maxilla raised superiorly. There were marked compressions in the fronto-maxillary suture. The articular process of the mandible tended to be translocated downwards. The experiment illustrates the far-reaching influence of the temporal muscle on the premaxillary node and its downwardly directed force at the level of the squamosal node.

(*f*) *Experiment* 13

Forces were applied by means of finger pressure on one side at the inferior margin of the mandible at the level of masseteric insertions, and were directed dorsally. This resulted in a pronounced compression along the fronto-maxillary suture. The maxillary node was translocated superiorly (Plate 1, Fig. 7*b*), the superior margin of the palatine bone being translocated in the same direction also. This experiment was designed to demonstrate the stresses which are evoked in the skull by pressure from the mandible during the contractions of the masseter.

(*g*) *Experiment* 14

This experiment was designed to represent the stresses which originate during the crushing of bones by carnivores. A rod was placed between the carnassial and the mandibular molar. Forces were applied on one side as in experiment 13, resulting in a very well-marked compression along the naso-maxillary suture. The frontal process of the maxillary bone was translocated medially (Fig. 1*D*). The fronto-lacrimal, fronto-maxillary, and fronto-sphenoid sutures were disjointed (Plate 1, Fig. 8), while the interpalatine and, to a lesser extent, the intermaxillary sutures, were widened.

(*h*) *Experiment* 15

Ventrally directed forces were applied by means of finger pressure on one side at the zygomatic process of the squamosal bone, just above the glenoid cavity (Fig. 2(*15*)). This test was designed to investigate the squamosal component of the masseter. They resulted in the disjointing of the sutures at the roof of the skull similar to those demonstrated in Figure 1*A*.

V. Provinces of the Muscles

Experiments 1-15 form a basis for the outlining of the sphere of the morphogenetic influences of the masseter as well as those of the temporal muscle. The areas of the skull which are influenced by the stresses originating from a single muscle are scattered throughout the skull and have no direct relation with the topography of the muscles and their insertions; such a set of areas is here called the "province" of that muscle. The provinces of the temporal and masseter muscles overlap each other. The areas of both provinces are demonstrated in Figure 3.

(*a*) *Province of the Masseter Muscle*

The province of the masseter (Fig. 3) covers the roof of the skull (expts. 1 and 8) where the tensorial stresses develop, the upper (frontal) part of the orbit (expt. 2) where the compressions may be detected, the maxillo-squamosal tract (expts. 2 and 3) with the well-marked tensorial stresses, and the roof of the anterior triangle (expts. 2 and 3) where

compression may occur. It also covers the glenoid cavity, where the stresses are directed laterally (expt. 9), medially (expt. 8), and posteriorly, and originate from the action of the masseter, and also the premaxillo-maxillary node and the zygomatic arch.

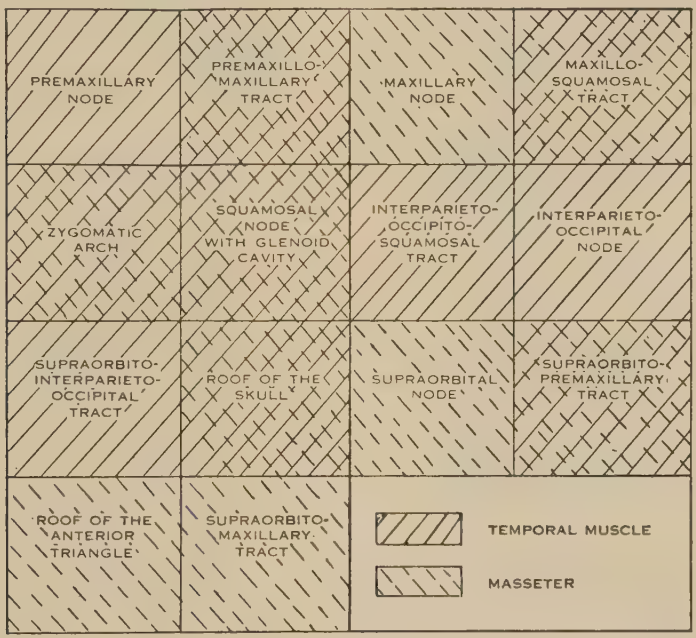


Fig. 3.—Provinces of the masseter and temporal muscles in the breviarcuate skull.

(*b*) *Province of the Temporal Muscle*

The province of the temporal muscle (Fig. 3) covers the zygomatic arch (expt. 4) where the anteriorly directed stresses appear, the maxillo-squamosal tract (expt. 4) where the temporal muscle indicates tensorial stresses as well as some compressions, the anterior triangle (expt. 12), and the glenoid cavity (expt. 12) (squamosal node). Finally, this muscle influences the interparieto-occipital node and the interparieto-occipito-squamosal tract.

VI. The Stresses in the Glenoid Cavity

In the light of this analysis, the glenoid cavity is a focus of the variety of stresses which resist one another (Figs. 4 and 5). The medially directed stress originates from the masseter of the same side (Fig. 4*a*) and is opposed by the vector resulting from the contraction of the masseter of the opposite side (Fig. 4*b*). The posteriorly directed stress (Fig. 4*c*) originates also from the masseter but this time it is opposed by the vector resulting from the contraction of the temporal muscle (Fig. 4*d*).

Similar opposition of stresses which results from the contraction of the temporal muscle and the masseter occurs in the dorso-ventral plane. The dorsally directed stresses result from the action of the masseter (Fig. 5*a*), while the dorso-ventral vector (Fig. 5*b*) is caused by the temporal muscle.

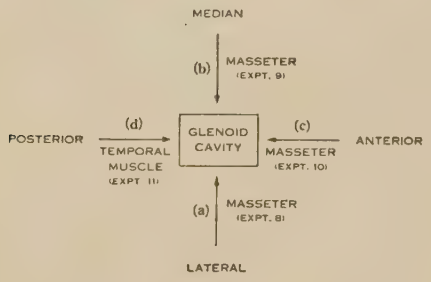


Fig. 4

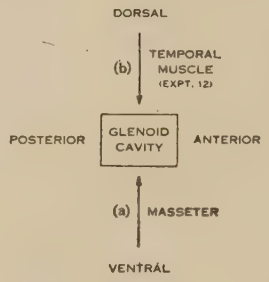


Fig. 5

Fig. 4.—Origin and distribution of vectors in the glenoid cavity of the dog during mastication. Arrows indicate the direction of stresses, which are in the transverse plane, and the muscles initiating these stresses.

Fig. 5.—As for Figure 4, but with stresses in the dorso-ventral plane.

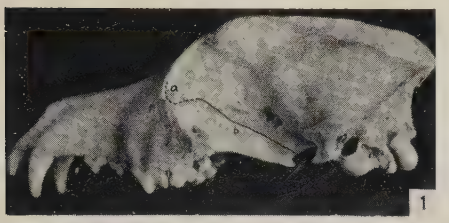
The origin of these opposing vectors in the glenoid cavity during the contraction of both muscles explains the occurrence and importance of the simultaneous use of main masticatory muscles even during unilateral biting (expt. 14), and also during the crushing of food in the anterior (premaxillary node) and posterior (maxillary node) positions. Experiment 14 also illustrates how the transverse stresses arise as a result of unilateral mastication which is so often observed in carnivores.

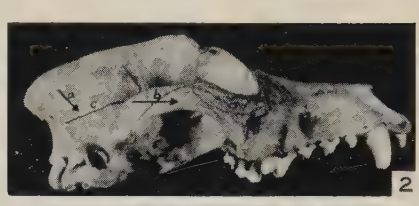
On the other hand, the composition of the vectorial system of the masticatory stresses within the glenoid cavity is facilitated by the innervation of all masticatory muscles (masseter, temporal, pterygoid, external, and internal) by the trigeminal nerve.

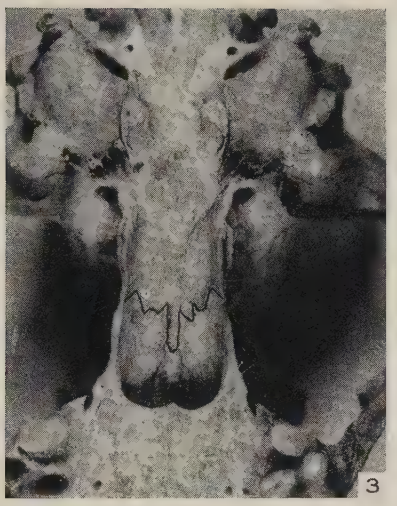
VII. Discussion

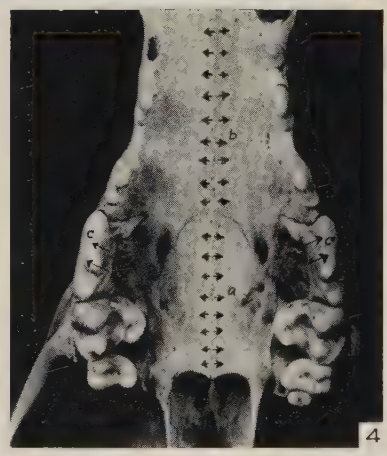
The results obtained from the experiments described above confirm the main analytical conclusions reached in Parts I-X of this series (Tucker 1954*a-f*, 1955*a-d*). The conditions of the experiments described in this paper were chosen in order to isolate the most basic stresses in the mammalian skull. One-half of the mandible only was used to obtain better contrast with that part of the skull not submitted to these stresses, and to observe the correlations of both cranial parameres. Rather strong evidence for the mechanical existence of the principal cranial arch is provided by experiments 3, 8, 9, and 10, which demonstrate the antero-posterior movements in the squamosal node (and glenoid cavity).

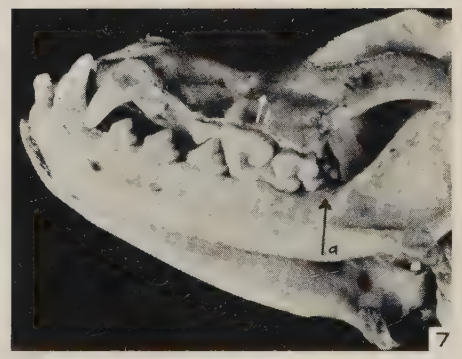
FUNCTIONAL AND ANALYTICAL CRANIOLOGY. XI

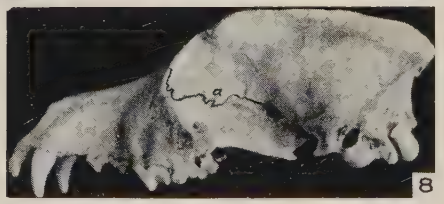


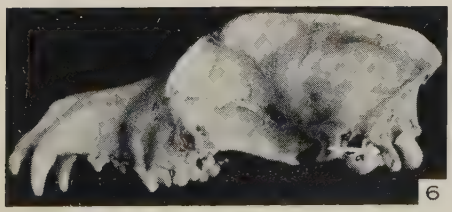












Experiment 15 was designed to observe the effects of the force directed downwards on the zygomatic process of the squamosal bone because this vector arises in the glenoid cavity and surroundings during the contraction of the temporal muscle (expt. 12). Because of its topographical position it should be opposed by the masseter.

VIII. References

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Explanation of Plate 1

The photographs do not demonstrate the actual skulls used in the experiments but indicate topography of stresses only.

Fig. 1.—Lateral view of the dog's skull. *a*, Fronto-lacrimal suture; *b*, loosening of the palato-sphenoidal connections.

Fig. 2.—Lateral view of the dog's skull. *a*, Application of forces; *b*, direction of movement of the zygomatic arch; *c*, squamoso-parietal connections.

Fig. 3.—Ventral view of the dog's skull. *a*, Widening of sutures; *b*, nodes.

Fig. 4.—Ventral view of the dog's skull. *a*, Stresses in the interpalatine suture; *b*, stresses in the intermaxillary suture; *c*, forces applied.

Fig. 5.—Ventral view of the dog's skull. *a*, premaxillo-maxillary suture; *b*, position of application of force.

Fig. 6.—Lateral view of the dog's skull. *a*, Direction of translocation of the glenoid cavity.

Fig. 7.—Ventral view of the dog's skull. *a*, Direction of application of force in experiment 13; *b*, direction of translocation of the maxilla.

Fig. 8.—Lateral view of the dog's skull. *a*, Topography of disjointing sutures.

Fig. 9.—Skull of the dog (left side, zygomatic arch removed) showing the positions of tracts and nodes in the breviarcuate skull (Tucker, 1954*a-f*). Arrows indicate the position of the forces applied at the cranial nodes during experiments 5 and 7.

STUDIES IN FUNCTIONAL AND ANALYTICAL CRANIOLOGY

XII. EXPERIMENTS WITH THE DECALCIFIED SKULL OF THE RABBIT

By R. TUCKER*

(*Manuscript received July* 19, 1955)

Summary

The decalcified skull of the rabbit was subjected to forces in a variety of ways and stresses were inferred from movements observed in sutures, nodes, and tracts. They were in accordance with the vectors analysed in previous studies (Tucker 1954*a-f*, 1955*a-d*, 1956*a*). The suspending arrangements of the maxillary alveolar processes in the rabbit were described.

I. INTRODUCTION

Experimental analysis of the decalcified skull was carried out on the skull of the rabbit as an example of the longoarcuate skull.

II. MATERIALS AND METHODS

The skull of the rabbit was decalcified in the same way as described previously for the dog (Tucker 1956*a*), and then submitted to a variety of forces.

III. REACTIONS OF THE DECALCIFIED SKULL

The complete skulls of three rabbits were submitted to the following tests:

(*a*) *Experiment* 1

This experiment was designed to provoke stresses in the longoarcuate skull similar to those which appear during the crushing of hard pieces of food by the incisors. Dorsally directed forces were applied by finger pressure at the premaxillary node (Fig. 1(*1*)). They resulted in disjunction of the premaxillo-maxillary suture and in compressions along the frontal processes of the premaxillary bones.

(*b*) *Experiment* 2

Forces tending to bend the skull laterally were applied at the level of the incisors (Fig. 1(*2*)). This experiment was designed to investigate the stresses set up by the lateral movements of the mandible. They resulted in the widening of the premaxillo-maxillary suture on the side of the skull to which force was applied, and in marked dorso-laterally directed compressions in the premaxillo-maxillary suture on the opposite side of

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the skull. The frontal process of the premaxillary bone of the opposite side is bent dorso-medially, while the anterior part of the maxilla is compressed dorso-laterally, resulting in lateral movement of the superior margin of the maxilla (Fig. 1(*2*)). The topography of these parts is shown in Plate 1, Figure 1.

Fig. 1.—Location of forces applied during experiments 1-6 and the topography of detectable stresses induced by them in the longoarcuate skull. Numbers correspond to the number of the experiment. Arrows indicate the direction of application of the forces. Symbols corresponding to these numbers (see legend) indicate the parts reacting.

(*c*) *Experiment* 3

This experiment was designed to investigate the mechanics of the masticatory node in the longoarcuate skull. Dorsally directed forces were applied by means of finger pressure at the maxillary node (Fig. 1(*3*)). They resulted in compressions in the postero-superior part of the maxilla and in the maxillo-frontal junction. The sutures of the maxillo-squamosal tract were widened. Moreover, the fronto-maxillary connections were disjointed, and their maxillary part translocated slightly laterally.

(*d*) *Experiment* 4

This experiment was designed to investigate stresses developed in the longoarcuate skull during the contractions of the zygomatic portion of the masseter. Ventrally directed forces were applied by means of finger pressure at the zygomatic arch behind the frontal process of the maxillary bone (Fig. 1(*4*)). They resulted in the development of anteriorly and laterally directed stresses in the maxillo-frontal connections, and in a slight tendency of the maxillary node to anterior translocation. The zygomatic arch was bent downwards.

(*e*) *Experiment* 5

Dorsally directed forces were applied by means of finger pressure in the glenoid cavity (Fig. 1(*5*)). They resulted in marked compressions of the squamosal bone above the zygomatic processes. The wall of the cranium below the glenoid cavity showed noticeable tensions. The experiment was designed to study the stresses in the glenoid cavity which may be induced by the articular process of the mandible during mastication.

(*f*) *Experiment* 6

Anteriorly and ventrally directed forces were applied by means of finger pressure at the junction of the squamosal and parietal bones (Fig. 1(*6*)). The maxillary node was kept in a fixed position. They resulted in compressions in the squamoso-maxillary tract, in the fronto-maxillary suture in the median part of the orbit, and also in the frontal process of the maxilla. This experiment was designed to study the postero-anterior vector which originates from the contraction of the temporal muscle.

IV. Reactions of the Decalcified Skull to Stresses Transmitted through the Mandible

(*a*) *Experiment* 7

The mandible, in normal position, was pressed against the skull to test the stresses arising in the skull during mastication by the pressure of the mandible. Compressions around the maxillary node and above the glenoid cavity resulted.

(*b*) *Experiment* 8

The mandible, in normal position, was subjected to such force as exists during the contraction of the temporal muscle. The changes in the skull were similar to those in experiment 7.

V. Discussion

(*a*) *The Connections of the Maxillary Node*

Experiment 3 shows the elastic connections of the maxillary node in the rabbit with the rest of the skull. The maxillary alveolar process does not contact any of the solid structures above it. In consequence, it is suspended by the perpendicular lamina of the palatine bone, the palatine process of the maxillary bone, the horizontal lamina of the palatine bone, the maxillo-premaxillary tract, the frontal process of the maxillary bone, the zygomatic arch, and, finally, the very thin fronto-maxillary connections (Fig. 2; Plate 1, Figs. 2 and 3).

(*b*) *Stresses in the Premaxillary Node*

The stresses in the premaxillary node, when investigated in a vertical plane, correspond roughly to those in the breviarcuate skull. However,

the vectors in the transverse plane which result from lateral movements of the mandible in rodents and lagomorphs cause marked differences in the pattern of stresses in the right and left side of the skull. The stresses in the premaxillary bones of the opposite halves of the skull change mutually. The results obtained in experiment 8 seem to point out one more peculiarity in the premaxillary node of the rabbit. This node is influenced less by the temporal muscle than it is in the breviarcuate skull. The masseter, which is translocated anteriorly, and the muscles which govern

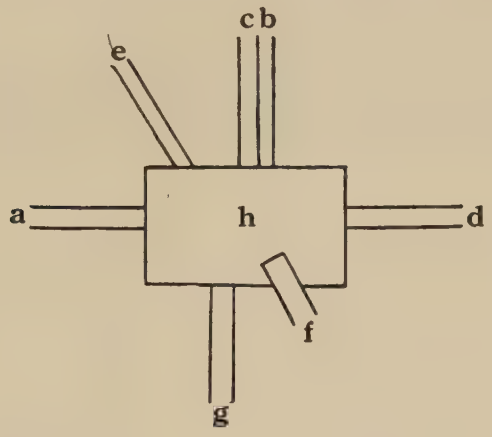

Fig. 2.—Connections of the maxillary alveolar process in the skull of the rabbit. Dorsal view, right side. *a*, Perpendicular lamina of the palatine bone; *b*, palatine process of the maxillary bone; *c*, horizontal lamina of the palatine bone; *d*, maxillo-premaxillary tract; *e*, fronto-maxillary connections; *f*, frontal process of the maxillary bone; *g*, zygomatic arch; *h*, maxillary alveolar process.

the lateral movements of the mandible (pterygoideus) are the most powerful source of vectors in the premaxillary node of the rabbit. Consequently, the temporal muscle is much more connected with the maxillary node than in carnivores. On the other hand, this diminution of the province of the temporal muscle could be explained by the morphology of the coronoid process in the mandible of lagomorphs (which is very poorly-developed and placed below the articular process of the mandible) as well as by the low position of the teeth at the level of the maxillary node.

VI. References

Tucker, R. (1954*a-f*).—Studies in functional and analytical craniology. I-VI. *Aust. J. Zool.* **2**: 381-430.

Tucker, R. (1955*a-d*).—Studies in functional and analytical craniology. VII-X. *Aust. J. Zool.* **3**: 513-44.

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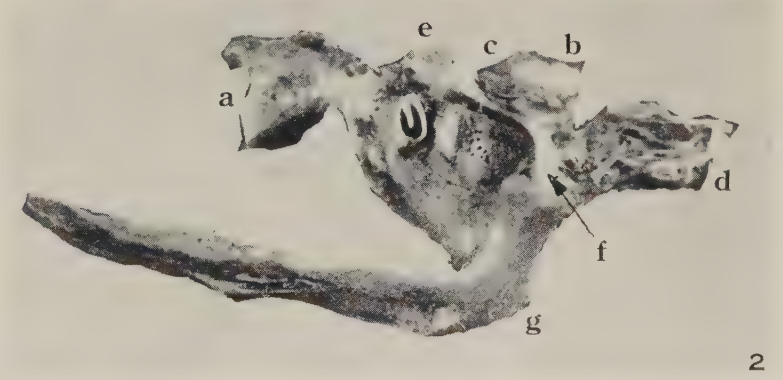
Explanation of Plate 1

Fig. 1.—Localizations of stresses resulting from pressing the incisors latero-medially in the rabbit's skull. *a*, Frontal process of the premaxillary bone; *b*, frontal process of the maxillary bone, *c*, superior margin of the maxilla; *d*, premaxillo-maxillary suture; *e*, maxillo-frontal junctions; *f*, postero-superior part of the maxilla.

Fig. 2.—Dorsal view of the maxillary node and its connections in the rabbit's skull. *a*, Perpendicular lamina of the palatine bone; *b*, palatine process of the maxillary bone; *c*, horizontal lamina of the palatine bone; *d*, maxillo-premaxillary tract; *e*, fronto-maxillary connections; *f*, frontal process of the maxillary bone; *g*, zygomatic arch. Orientation as in Figure 1 above.

Fig. 3.—Lateral view of the right maxillary node and its connections in the rabbit's skull. *a*, Perpendicular lamina of the palatine bone; *d*, maxillo-premaxillary tract; *e*, fronto-maxillary connections; *f*, frontal process of the maxillary bone; *g*, zygomatic arch. Orientation as in Figure 1 above.

FUNCTIONAL AND ANALYTICAL CRANIOLOGY. XII



STUDIES IN FUNCTIONAL AND ANALYTICAL CRANIOLOGY

XIII. EXPERIMENTS WITH THE DECALCIFIED SKULL OF THE CALF

By R. TUCKER*

(*Manuscript received July* 19, 1955)

Summary

Stresses in the calf's skull were investigated experimentally, using a decalcified skull. In the margin of the orbit most of the stresses originating from the masticatory muscle oppose each other.

I. INTRODUCTION

Experimental analysis of the decalcified skull was carried out on the skull of the calf as an example of the planoarcuate skull.

II. MATERIAL AND METHODS

Two whole skulls and one half skull of the calf were prepared and preserved in the way previously described for the dog (Tucker 1956*a*).

III. REACTIONS OF THE DECALCIFIED SKULL

(*a*) *Experiment* 1

Force was applied by means of finger pressure at the zygomatic arch just behind the frontal process of the zygomatic bone (Fig. 1), and directed ventrally, thus imitating the force exerted by the zygomatic insertions of the masseter. It resulted in the zygomatic arch bending downwards and the zygomatico-frontal and zygomatico-squamosal sutures becoming disjointed. The maxillary node was pushed slightly forwards, with the premaxillary node translocated a little superiorly (Figs. 1 and 6(*1*)).

(*b*) *Experiment* 2

Force was applied by means of finger pressure at the postorbital process of the frontal bone, and directed ventrally. The test was designed to provoke stresses similar to those transmitted from the zygomatic arch towards the frontal bone during the contractions of the masseter. Antero-ventrally directed compressions in the lacrimo-frontal and lacrimo-maxillary sutures resulted (Figs. 2*a*, *b* and 6(*2*)). The maxillary node was pressed downwards (Fig. 2*c*).

(*c*) *Experiment* 3

Force was applied by means of finger pressure to the parietal bone at the insertions of the temporal muscle, and directed anteriorly and

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ventrally, thus corresponding to the anterior vector originating from the contractions of the temporal muscle (Fig. 6(*3*)). It resulted in the anterior translocation of the squamoso-zygomatic and fronto-zygomatic connections, and in marked compressions along the fronto-lacrimal and fronto-maxillary sutures.

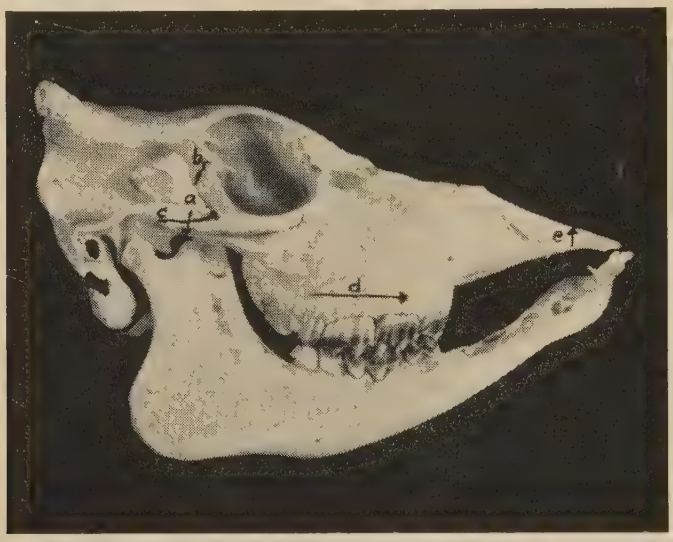


Fig. 1.—Lateral view of the calf's skull illustrating topographical changes in experiment 1. *a*, Direction of application of force in experiment 1; *b*, zygomatico-parietal suture; *c*, zygomatico-squamosal suture; *d*, direction of movement of the maxillary node in experiment 1; *e*, direction of movement of the premaxillary node in experiment 1.

(*d*) *Experiment* 4

Force was applied by pressing the premaxillary node dorsally (Fig. 6(*4*)). Forces of this kind are present wherever the mandibular incisors press against the premaxillary node. It resulted in compression in the maxillo-lacrimal and lacrimo-frontal sutures, and in marked widening of sutures in the premaxillo-maxillary connections and along the maxillo-squamosal tract.

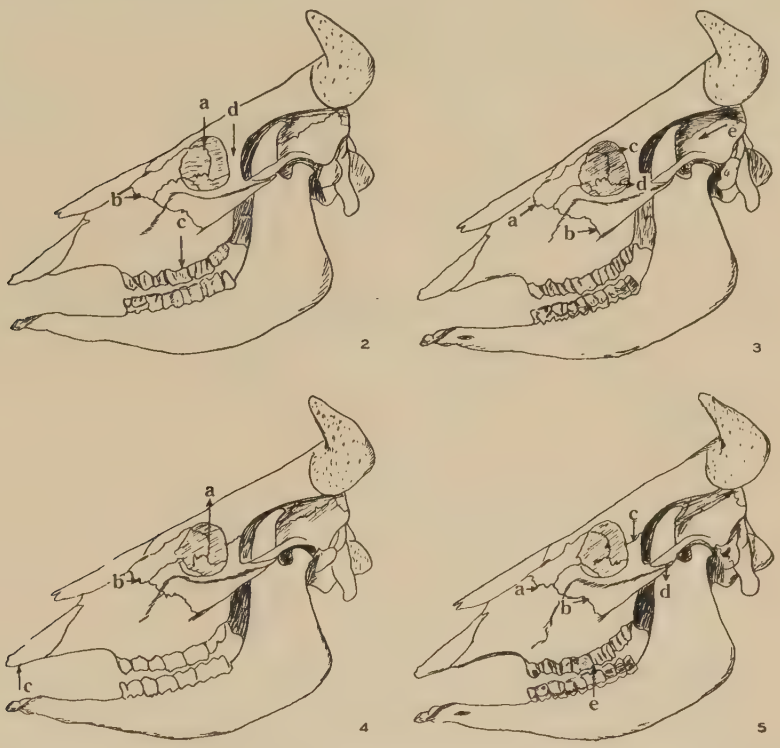
(*e*) *Experiment* 5

Dorsally directed forces were applied by means of finger pressure to the maxillary node thus representing the vectors which originate from both main masticatory muscles during mastication (Fig. 6(*5*)). They resulted in compressions at the level of the lacrimo-maxillary, zygomatico-maxillary, and fronto-lacrimal connections (Fig. 3).

IV. Reactions of the Decalcified Skull to Stresses Transmitted through the Mandible

(*a*) *Experiment* 6

This experiment was a modification of experiment 5. Force was applied at the mandible while the mandible pressed against the skull (Fig. 6(*6*)). Compressions in the fronto-lacrimal and maxillo-lacrimal sutures were clearly visible.



Lateral view of the calf's skull illustrating topographical changes in experiments 2-5.
Fig. 2.—*a*, Lacrimo-frontal suture; *b*, lacrimo-maxillary suture; *c*, direction of the maxillary translocation; *d*, direction of application of force in experiment 2.
Fig. 3.—*a*, Lacrimo-maxillary suture; *b*, zygomatico-maxillary suture; *c*, lacrimo-frontal suture; *d*, fronto-maxillary suture; *e*, direction of application of force in experiment 3.
Fig. 4.—*a*, Direction of translocation in the lacrimo-frontal suture; *b*, lacrimo-maxillary suture; *c*, direction of application of force in experiment 4.
Fig. 5.—*a*, Maxillo-lacrimal connections; *b*, maxillo-zygomatic connections; *c*, zygomatico-frontal connections; *d*, zygomatico-squamosal connections; *e*, direction of application of force in experiment 5.

(*b*) *Experiment* 7

Forces, directed dorso-posteriorly, were applied by means of finger pressure at the temporal (coronoid) process of the mandible, thus repre-

senting forces exerted by the contractions of the temporal muscle. Changes similar to those in experiment 6 resulted (Fig. 6(*7*)).

(*c*) *Experiment* 8

This experiment was designed to investigate the stresses resulting from the horizontal movements of the mandible of the ruminant. The mandible contacting the maxillary teeth was moved medially (Fig. 6(*8*)). This resulted in an upward movement of the lacrimo-frontal suture, and also marked compressions in the lacrimo-maxillary (Fig. 4), interpalatine, and inter-maxillary sutures (Fig. 6(*8*)).

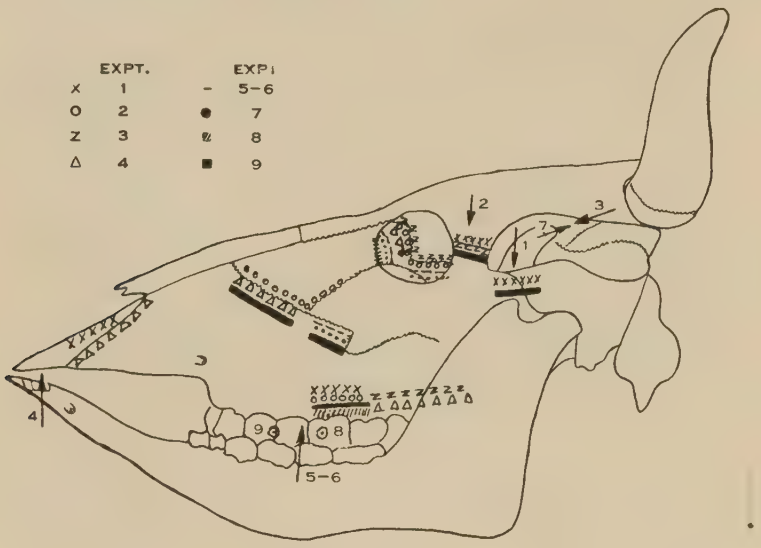


Fig. 6.—Location of forces applied during experiments 1-9, and the topography of detectable stresses induced by them in the planoarcuate skull. Numbers correspond to the number of the experiment. Symbols corresponding to these numbers (see legend) indicate the parts reacting.

(*d*) *Experiment* 9

The design of this experiment was similar to experiment 8, but movements in another direction were investigated. The mandible contacting the maxillary teeth was moved laterally. This resulted in compressions in the maxillo-lacrimal, maxillo-zygomatic, zygomatico-frontal, and zygomatico-squamosal sutures (Figs. 5 and 6(*9*)). The intermaxillary and interpalatine sutures were widened.

V. Discussion

Most of the results of these experiments, described in the light of previous analyses (Tucker 1954*a-f*, 1955*a-d*, 1956*a, b*), now appear self-explanatory. However, they have given additional knowledge about the

distribution of stresses, especially around the orbit, and the opposing stresses which are so common in this region of the breviarcuate skull.

With reference to the action of the temporal muscle, the planoarcuate skull has some similarity to the longoarcuate skull in that the temporal muscle does not have such importance in the quick movements of the mandible and the stresses located in the premaxillary node. The weak development of the temporal (coronoid) process of the mandible in ruminants as against those of Carnivora is further evidence of this fact. In the rabbit, the coronoid process is not developed and the articular process has only its anterior part placed in the glenoid cavity.

Experiments 8 and 9 were performed to investigate the stresses originating in the lateral movements of the mandible during mastication in ruminants.

VI. References

Tucker, R. (1954*a-f*).—Studies in functional and analytical craniology. I-VI. *Aust. J. Zool.* **2**: 381-430.

Tucker, R. (1955*a-d*).—Studies in functional and analytical craniology. VII-X. *Aust. J. Zool.* **3**: 513-44.

Tucker, R. (1956*a, b*).—Studies in functional and analytical craniology. XI, XII. *Aust. J. Zool.* **4**: 40-9, 50-4.

STUDIES IN FUNCTIONAL AND ANALYTICAL CRANIOLOGY

XIV. EXPERIMENTS WITH THE DECALCIFIED SKULL OF THE LEAF MONKEY

By R. TUCKER*

(*Manuscript received July* 19, 1955)

Summary

The skull of the monkey was analysed experimentally. The strains around the supraorbital node differ from those in the calf (Tucker 1956*c*). The lateral wall of the brain case shows depressions related to the forces applied in the glenoidal cavity. The palatine bone in the monkey is replaced functionally by the lateral pterygoid lamina in the squamoso-maxillary tract. Three functionally different areas at the base of the skull are described and illustrated.

I. INTRODUCTION

Experimental analysis of the decalcified skull was carried out on the skull of the monkey as an example of the primate skull.

II. MATERIAL AND METHODS

The skull of a leaf monkey was prepared and preserved in the way previously described for the dog (Tucker 1956*a*).

III. REACTIONS OF THE DECALCIFIED SKULL

(*a*) *Experiment* 1

Forces were applied by means of finger pressure at the zygomatic arch, and were directed downwards behind the fronto-zygomatic connections (Plate 1, Fig. 1*a*). This experiment was designed to induce the stresses which normally arise from the contractions of the masseter. They resulted in tensile strains in the fronto-maxillary connections, particularly visible in the internal margin of the external part of the orbit, in the superior part of the orbit, and along the frontal crest. Compressive strains, as demonstrated by an extrusion of the bony parts, appeared in the lower part of the orbita and in the maxillary bone (Plate 1, Fig. 1).

(*b*) *Experiment* 2

Dorsally directed forces were applied to the glenoid cavity (Plate 1, Fig. 2*a*). This experiment was designed to investigate the stresses which result from the pressing of the articular process of the mandible against the zygomatic process of the squamosal bone. This resulted in the formation of depressions (Plate 1, Fig. 2*b*) in the squama and the superior translocation of the glenoid cavity and the post-glenoidal process (Plate 1,

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Fig. 2). Tensile stresses appeared in the area bounded by the spheno-zygomatic curvature and the squamoso-petrosal suture (Plate 1, Fig. 5*a*, *c*).

(*c*) *Experiment* 3

Forces were applied to the glenoid cavity by means of finger pressure and were directed postero-dorsally (Plate 1, Fig. 4*a*). The experiment was designed to test the postero-dorsal vector which should normally result from the pressing of the articular process of the mandible postero-dorsally. The application of these forces resulted in the widening of the squamoso-zygomatic suture, the lateral translocation of the zygomatic process of the squamosal bone, the appearance of tensorial strains along the sphenoidal part of the spheno-zygomatic curvature, and compressions along the sustentaculum. A depression was formed in the brain case at the superior end of the sustentaculum (Plate 1, Figs. 4 and 5).

(*d*) *Experiment* 4

With the maxillary node in a fixed position, antero-ventrally directed forces were applied by means of finger pressure to the parietal bone in the area covered by the temporal muscle to provoke the antero-ventral vector which originates by the contraction of the temporal muscles (Plate 1, Fig. 4*d*). They resulted in compressive strains occurring in the surroundings of the postcrestal fossa, in the lateral pterygoid lamina, in the perpendicular lamina of the palatine bone, and in the slightly anterior translocation of the squamosal node (Plate 1, Fig. 4).

(*e*) *Experiment* 5

Forces, representing those normally induced in the premaxillary node during biting and mastication, were applied by means of finger pressure at the premaxillary node, and were directed dorsally (Plate 1, Fig. 3*a*). They resulted in the widening of the apertura nasalis, in a marked dorsally directed translocation of the lacrimal bone and the surrounding part of the orbit, in tensile strains along the premaxillo-maxillary connections, and in compressive strains in the dorsal part of the nose (Plate 1, Fig. 3).

(*f*) *Experiment* 6

Dorsally directed forces were applied by means of finger pressure at the maxillary node (Plate 1, Figs. 2*c* and 4*g*). These forces normally occur during mastication. They resulted in the superior translocation of the maxilla, the lacrimal bone being greatly translocated in a dorso-lateral direction. The compressive strains were in the frontal process of the maxilla and along the frontal process of the malar bone (external part of the orbita). Tensile stresses were located along the perpendicular lamina of the palatine bone, the lateral pterygoid lamina, and the palato-maxillary connections which form a part of the maxillo-squamosal tract. Similar

strains may be traced along the squamoso-petrosal suture (the static trabecula). If the pressure is not symmetrical, the intermaxillary suture is also disjointed (Plate 1, Fig. 5).

(*g*) *Experiment* 7

Forces were applied by means of finger pressure at the maxillary node and in the region of the glenoid cavity simultaneously. The experiment was designed to simulate the appearance of the secondary stresses (Tucker 1954*a*) in the skull during mastication. They resulted in great tensorial strains in the squamoso-maxillary tract, and the palato-maxillary and the palato-pterygoid sutures were disjointed. Similar strains were also visible in the spheno-zygomatic curvature (Plate 1, Fig. 5), while compressions were found at the base of the orbit.

IV. Reactions of the Decalcified Skull to Stresses Transmitted through the Mandible

(*a*) *Experiment* 8

Forces, directed dorsally and posteriorly, were applied by means of finger pressure at the temporal (coronoid) process of the mandible to represent the dorso-caudal vector originating from the contraction of the masseter. They resulted in the posterior bending of the post-glenoidal processes, in compressive strains along the sustentaculum, and also in dorsally directed compressive strains in the maxillary node.

(*b*) *Experiment* 9

The mandible, in its anatomical position, was pressed against the skull, as normally occurs if the mouth is closed with some force. This resulted in compressive strains in the glenoid cavity and in the region directly above it, in compressions on the maxillary node, in the lateral translocation of the lacrimal bone and the median wall of the orbit. Tensorial strains appeared in the maxillo-squamosal tract. The sutures around the lateral pterygoid lamina were disjointed.

V. The Biomechanical Characteristics of the Primate Skull

The experimental analysis of this variety of the planoarcuate skull results in the addition of new details with regard to the biomechanical importance of the orbit. The stresses and strains in the orbit and in the fronto-zygomatic connections were pointed out in discussion concerning the experimental analysis of the cranium of the calf (Tucker 1956*c*). However, it is shown here more distinctly that the lacrimal bone, the medial wall of the orbit, and the inferior part of the orbit can be exposed to the stresses originating from the masticatory movements.

The skull of primates demonstrates a different type of distribution of stresses around the supraorbital node. The stresses are not only trans-

mitted posteriorly by means of the frontal processes but also medially through the salient superior part of the orbit.

Another biomechanical characteristic of the primate skull is the presence of compressive stresses in the lateral wall of the brain case which results from the action of the masseter (expt. 2). The role of the sustentaculum during the contraction of the temporal muscle is demonstrated by experiment 3. Similar results were also obtained in experiment 8. The characteristic reduction of the nasal bones results in an increase in the mechanical importance of the premaxillary bone around the apertura nasalis (expt. 5).

The maxillo-squamosal tract has the same function as that in other skulls, but is shaped a little differently. It is in agreement with the results previously obtained (Tucker 1955*c*) that, with reference to the masticatory stresses, the origin of structures which take part in the cranial tracts is more variable than is its function. In the analysed skull, the squamoso-maxillary tract has basically the same function as in the dog, but the perpendicular lamina of the palatine bone, which is so prominent in the dog, is here to a great extent replaced by the lateral pterygoid lamina. The area bounded laterally by the spheno-zygomatic curvature, medially by the lateral pterygoid lamina, and postero-medially by the squamoso-petrosal suture corresponds with the area of static trabeculae in the dog (Plate 1, Fig. 6 (oblique lines)). This area may be medially extended to the medial pterygoid lamina. Accordingly, the skull, when inspected ventrally, exposes three distinct functional regions (Plate 1, Fig. 6)—the first connected with the maxillary node (*a*), the second with the transmitting structures (*b*), and the third with the post-glenoidal and post-trabecular region (*c*).

VI. References

Tucker, R. (1954*a-f*).—Studies in functional and analytical craniology. I-VI. *Aust. J. Zool.* **2**: 381-430.

Tucker, R. (1955*a-d*).—Studies in functional and analytical craniology. VII-X. *Aust. J. Zool.* **3**: 513-44.

Tucker, R. (1956*a-c*).—Studies in functional and analytical craniology. XI-XIII. *Aust. J. Zool.* **4**: 40-59.

Explanation of Plate 1

All figures demonstrate the topography of described strains but not the actual strains and changes in the skull used in the experiments.

Fig. 1.—Distribution of strains after application of force at the zygomatic arch. *a*, Direction and location of force applied in experiment 1; *b*, tensile strains; *c*, compressive strains.

Fig. 2.—Lateral view of the skull of a monkey (left side). *a*, Direction and location of the force applied in experiment 2; *b*, depression in the squama; *c*, direction and location of the force applied in experiment 6.

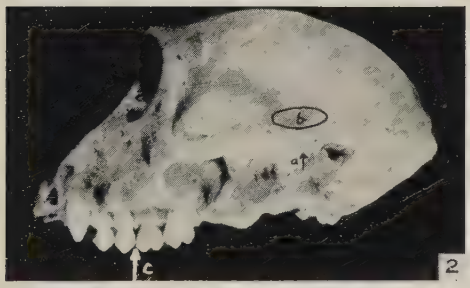
Fig. 3.—Distribution of strains after application of force to the premaxillary node. *a*, Direction and location of the force applied in experiment 5; *b*, widening of the apertura nasalis; *c*, area of translocation (see text); *d*, premaxillo-maxillary connections; *e*, compressive strains.

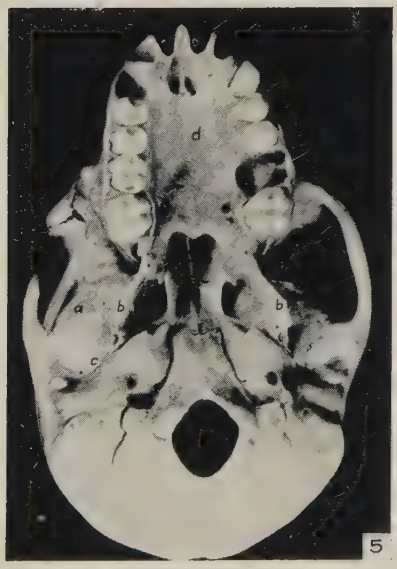
Fig. 4.—Lateral view of the skull of a monkey (right side). *a*, Direction and location of the force applied in experiment 3; *b*, compressions and *c*, depressions resulting from the force applied; *d*, direction and location of the force applied in experiment 4; *e*, postcrestal fossa; *f*, lateral pterygoid lamina; *g*, direction and location of the force applied in experiment 6.

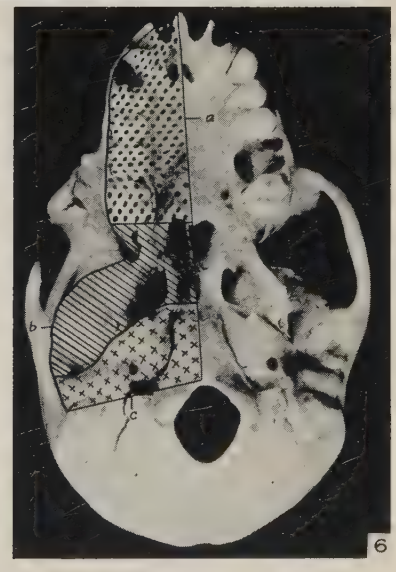
Fig. 5.—Ventral view of the skull of a monkey. *a*, Spheno-zygomatic curvature; *b*, lateral pterygoid lamina; *c*, squamoso-petrosal suture; *d*, intermaxillary suture.

Fig. 6.—Ventral view of the skull of a monkey. *a*, Functional area connected with the maxillary node; *b*, transmitting structures; *c*, postorbital area.

FUNCTIONAL AND ANALYTICAL CRANIOLOGY. XIV







THE GENUS *DROSOPHILA* (DIPTERA) IN EASTERN QUEENSLAND

II. SEASONAL CHANGES IN A NATURAL POPULATION 1952-1953

By W. B. MATHER*

(*Manuscript received September*, 1955)

Summary

The quantitative variations of 16 species of *Drosophila* attracted to banana bait at a single station over a period of 15 months have been assessed. There are two "abundant" winter species; other species fall into "common" and "rare" categories and flourish in either the autumn or spring. Peaks in the numbers of each species correspond either to the period of greatest rainfall, or the period of rising temperatures. Results have been compared with a similar survey at Aldrich Farm, Texas, U.S.A. (Patterson 1943).

D. novopaca, nom. nov. and *D. novamaculosa*, nom. nov. are proposed to replace the homonyms *D. opaca* Mather and *D. maculosa* Mather. *D. levis* Mather is synonymized with *D. bryani* Mall.

I. INTRODUCTION

In order to provide a background for experimental work on the genus *Drosophila* from south-eastern Queensland the following survey was undertaken. The initial aim was to determine the associations and relative numbers of species, which, in a given area, are attracted to banana bait,† and the extent to which these may vary through the year. The experiment has been based on similar work carried out at Aldrich Farm, Texas, U.S.A. (Patterson 1943).

Species collected in the present survey are those recently reviewed (Mather 1955). However, Dr. A. H. Sturtevant (personal communication) has indicated that the specific names *D. opaca* (Mather 1955, p. 558) and *D. maculosa* (Mather 1955, p. 560) are preoccupied by species originally described in the genus *Drosophila*. These species are now known as *Diathoneura opaca* (Williston) (Sturtevant 1942, p. 27) and *Leucophenga maculosa* (Coquillet) (Sturtevant 1921, p. 60). The names *D. novopaca*, nom. nov. and *D. novamaculosa*, nom. nov. are therefore erected to replace the homonyms *D. opaca* Mather and *D. maculosa* Mather respectively.

D. levis Mather (Mather 1955) has been found to be morphologically identical with specimens from a culture of *D. bryani* Mall. (Malloch 1934) from the Marshall Islands collected and identified by M. R. Wheeler, University of Texas. Upon re-examination of all published descriptions of both species it is now apparent that *D. levis* Mather is synonymous with *D. bryani* Mall.; and that this species is a member of the *levis* species group as previously defined (Mather 1955).

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† The standard method for collection of *Drosophila* (Patterson 1943).

II. Collection

(a) *Site*

The University Farm, Moggill, Brisbane, was selected for the following reasons: (1) variety of vegetation which should support a varied *Drosophila* fauna in a semi-natural state (see Appendix I) ; (2) convenient distance from the University (12 miles) ; and (3) being private property, it is not subjected to excessive disturbance.

The area sampled lies at the bottom of a gully running roughly north-east—south-west and flanked by slopes carrying open eucalypt forest and a considerable number of species of trees and shrubs (see Appendix I). Through the gully runs a small stream discharging into the Brisbane River.

(b) *Methods*

Cans of fermenting banana were set up and collections made therefrom at regular intervals (usually of 1 week) by sweeping over them with a hand net. Particular care was taken to collect the maximum number of flies at the bait at each collection. The cans measured 8 in. high by 7 in. diameter and were provided with a hinged lid to protect the bait from rain and desiccation. Staking to the ground was necessary to prevent the cans being upset (by horses and cows). The baits consisted of 2 lb of whole banana mashed up with a small quantity of baker's yeast. With this bait, the insects collected in the net were almost exclusively *Drosophila* spp.

Four baits were utilized, in similar shady situations, arranged in a rough rectangle approximately 100 × 200 yd. The cans were left continuously in the field for 15 months but the baits were changed weekly, immediately after collection, and the old bait removed from the farm to avoid artificial upsetting of the population.

All collections were made in the late afternoon because in Brazil (Pavan, Dobzhansky, and Burla 1950) and in the present series of investigations there is a diurnal fluctuation in the number of *Drosophila* species attracted to the baits with a peak in the late afternoon.

(c) *Treatment of Data*

As the number of collections in each month was increased from November 1952, the year October 1952-September 1953 has been chosen to estimate relative abundance of species and population fluctuation (Table 1). The females of *Drosophila melanogaster, D. simulans, D. serrata, D. takahashii,* and *D. dispar* have been treated as a complex, as they are difficult to distinguish. Similarly females of *D. repleta* and *D. versicolor* were not distinguished.

III. Results

(a) *Species Collected*

The species collected, which have recently been reviewed (Mather 1955) are listed, together with mean monthly temperatures and rainfalls,

in Table 1. The climatic data have been supplied by the Queensland Meteorological Bureau, and are for Brisbane, 7 miles north-east from Moggill. Taxonomically, three subgenera are represented, the prevalence of the subgenus *Pholadoris* being of interest.

On the basis of abundance of males for the year October 1952-September 1953, the species may be classified as follows:

"Abundant": *D. simulans* (63%), *D. serrata* (21%)

"Common": *D. takahashii* (4%), *D. lativittata* (4%), *D. immigrans* (2%), *D. hydei* (2%), *D. versicolor* (1%), *D. melanogaster* (1%), *D. enigma* (1%), *D. repleta* (1%)

"Rare": *D. cancellata* (0.1%), *D. novamaculosa* (0.05%), *D. novopaca* (0.025%), *D. dispar* (0.025%), *D. busckii* (0.025%), *D. bryani* (0%).*

The percentages of abundant and common species varied little at each bait at any one time. Rare species, however, were not always present at each of the four baits simultaneously. Species taken represent all species which have previously been recorded from the Brisbane area.

(*b*) *Population Fluctuation*

With the 10 more common species, sufficient individuals were caught to calculate monthly frequencies over a complete year (Oct. 1952-Sept. 1953) (see Table 2).

As the number of collections made per month varied, it was necessary with each species to divide the total for the month by the number of collections made in that month, and to use these derived figures for the calculation of monthly frequencies.

The species segregate into five groups representing the time of their maximum numbers:

(i) Spring species: *D. hydei, D. repleta,* and *D. versicolor*

(ii) Autumn species: *D. simulans*

(iii) Spring and autumn species: *D. serrata*

(iv) Winter species: *D. enigma, D. takahashii, D. immigrans,* and *D. lativittata*

(v) Species present in all seasons: *D. melanogaster.*

D. lativittata and *D. enigma* have not been taken in northern Queensland (Mather 1955). As these species flourish at Moggill Farm only during the colder months, it may be assumed that they are temperate rather than tropical species.

With the seven rarer species, it will be noted that *D. novopaca* was collected in summer, *D. bryani* in autumn and winter, *D. dispar* in winter,

* *D. bryani* females only were taken (see Table 1).

TABLE 1

COLLECTION RECORDS FOR MOGGILL FARM

Subgenus	Species	1952 July ♂	July ♀	Aug. ♂	Aug. ♀	Sept. ♂	Sept. ♀	Oct. ♂	Oct. ♀	Nov. ♂	Nov. ♀	Dec. ♂	Dec. ♀
Pholadoris	*D. cancellata*						2			4	5		
	D. enigma		1	1	1	3	4			1	1		
	D. lativittata	3		20	22	1	14	1		8	7		
	D. novopaca												
	D. novamaculosa									2	5	2	
	D. bryani												
Sophophora	*D. busckii*	4		7	1	2	4						
	D. melanogaster	2		3		2		1		13		5	
	D. simulans	77		225		157		33		87		16	
	D. serrata		47	13	148	2	130	7	14	58	81	19	30
	D. takahashii	1		6									
	D. dispar												
Drosophila	*D. hydei*					1	3	1	2	43	39	8	3
	D. repleta					1		1		41			
	D. versicolor								2	24	21	11	1
	D. immigrans	1				9	11	1	5	1			
	Totals	136		447		346		68		441		95	
Number of collections		2		2		2		2		6		5	
Average number/collection		68		223		173		34		73		19	
Mean temperature (°F)		58.7		60.6		65.1		69.7		73.3		76.0	
Rainfall (in.)		1.07		1.80		0.92		3.78		2.34		2.74	
Mean normal temperature (°F)		59.5		62.3		64.6		69.3		75.1		76.4	
Normal rainfall (in.)		2.15		1.83		1.96		2.68		3.70		4.97	

TABLE 1 (*Continued*)

Subgenus	Species	1953 Jan. ♂	Jan. ♀	Jan.	Feb. ♂	Feb. ♀	Feb.	Mar. ♂	Mar. ♀	Mar.	Apr. ♂	Apr. ♀	Apr.	May ♂	May ♀	May	June ♂	June ♀	June	July ♂	July ♀	July	Aug. ♂	Aug. ♀	Aug.	Sept. ♂	Sept. ♀	Sept.
Pholadoris	*D. cancellata*										1	1																
	D. enigma										3	1		3	8		13	13		2	7			2				
	D. lativittata		2			3		19	13		8	7			4		2	2		29	22		50	31		29	22	
	D. novopaca				1	1																						
	D. novamaculosa											1																
	D. bryani											1			1													
Sophophora	*D. busckii*																						1					
	D. melanogaster	2			2			7			3			1			1									3		
	D. simulans	19			148			641			551			328			491			69			40			40		
	D. serrata	26		18	117		94	182		506	147		301	39		240	16		407	23		81	28		41	146		109
	D. takahashii				1			8			20			25			51			34			10			4		
	D. dispar																			1								
Drosophila	*D. hydei*	5	5					1			2	3		2	1		1											
	D. repleta						3																					2
	D. versicolor	8			1			1															1			3		
	D. immigrans							6	14		6	4		15	8		39	47		8	5		9			6	11	
	Totals		85			371			1398			1040			675			1083			281		213			375	
Number of collections			4			3			5			3			2			4			4		4			4		
Average number/collection			21			124			279			347			337			271			70		53			94		
Mean temperature (°F)			77.1			76.5			74.3			70.1			64.6			60.2			58.7		60.6			68.1		
Rainfall (in.)			5.98			14.41			5.44			1.87			0.93			0.12			0.05		3.66			0.56		
Mean normal temperature (°F)			74.4			74.9			73.3			72.1			64.9			60.3			59.5		62.3			64.6		
Normal rainfall (in.)			6.36			6.35			5.75			3.62			3.69			2.65			2.15		1.83			1.96		

TABLE 2

PERCENTAGE POPULATION FLUCTUATION OF SELECTED SPECIES

Species	1952			1953								
	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.
D. enigma		2.0					8.1	33.5	40.0	13.7	3.0	
D. lativittata	0.8	3.8	0.6	0.8	1.5	10.0	8.0	3.1	1.5	20.0	31.0	20.0
*D. melanogaster**	5.7	25.0	11.5	5.7	7.7	16.0	11.5	5.7	2.9			8.6
*D. simulans**	2.3	2.0	0.4	0.7	6.8	17.6	25.5	22.8	16.9	2.4	1.4	1.4
*D. serrata**	1.6	4.4	1.8	3.0	17.7	16.5	22.3	8.9	1.8	2.6	3.2	16.6
*D. takahashii**					0.7	3.5	14.3	27.3	27.9	18.6	5.5	2.2
D. hydei	5.4	57.0	9.3	11.0		0.8	7.1	8.4	1.1			
*D. repleta**	6.8	93.0										
*D. versicolor**		41.0	22.7	20.6	3.1	2.6					2.6	7.7
D. immigrans	5.6	0.4				7.5	6.2	21.6	40.0	6.1	4.2	8.0

* Calculated on males only.

D. busckii in winter and spring, and *D. cancellata* and *D. novamaculosa* in spring and autumn. However, as only small numbers of these species were taken at any time, they may have been missed in other seasons.

(*c*) *Sex Ratio*

A very marked discrepancy between the sexes is apparent (Table 3); 63 per cent. of the total specimens caught were males, and with one exception (*D. immigrans*), this occurs in every species where adequate numbers were collected. Whether this is due to a real preponderance of males or whether there is a differential attraction to, or tendency for males to remain at, the baits, is uncertain.

TABLE 3

DROSOPHILA SPECIES: SEX RATIO

Species	Males and Females	Males	Females	Males (%)	Females (%)
D. cancellata	13	5	8		
D. enigma	64	26	38		
D. lativittata	321	172	149	54	46
D. novopaca	2	1	1		
D. novamaculosa	8	2	6		
D. bryani	2	0	2		
D. busckii	19	14	5		
D. melanogaster	6198	45	2247	64	36
D. simulans		2922			
D. serrata		823			
D. takahashii		160			
D. dispar		1			
D. hydei	120	64	56	53	47
D. repleta	121	43	29	76	24
D. versicolor		49			
D. immigrans	206	101	105	49	51
Totals	7074	4428	2654	63	37

IV. DISCUSSION

To what extent the population fluctuations, as indicated by the banana-bait method, reflect the actual population fluctuations of the species is at the present time unknown, since, although banana has been shown to be the best bait for attracting a maximum number of species and in large quantities, the proportion of species attracted with different baits does actually vary (Spencer 1950). However, the results are considered as true for that portion of the population which is attracted to this bait.

Of the 10 abundant and common species taken, four (*D. enigma, D. takahashii, D. immigrans, D. lativittata*) increased during winter, and two species, *D. simulans* and *D. serrata,* increased during the autumn.

These species all contributed to the major peak of the total *Drosophila* population which was reached in April. In August 1952 and September 1953 increasing numbers of the spring species, *D. hydei, D. repleta, D. versicolor,* and *D. serrata,* created, with the declining *D. simulans,* another peak in the population. The spring species then continued to increase, although they never reached very great numbers, to create the small November population peak.

Consideration of climatic data (Table 1) shows that the winter-autumn species peak follows the peak in the annual rainfall; and it is possible that these species flourish with the lush vegetation produced by this high rainfall coupled with the moderate temperatures. The spring

TABLE 4

FRUITS WITH WHICH DROSOPHILA SPECIES MAY BE ASSOCIATED

Fruiting Season	Species	Origin
All seasons	*Cassytha pubescens* R.Br.	Indigenous
Summer	*Elaeocarpus obovatus*	Indigenous
Summer	*Paspalum dilatatum**	Brazil
Summer and autumn	*Cudrania javanensis*	Indigenous
Summer and autumn	*Eustrephus latifolius*	Indigenous
Summer and autumn	*Passiflora suberosa*	Brazil
Summer and autumn	*Passiflora alba*	Brazil
Summer–winter	*Cryptocarya triplinervis*	Indigenous
Autumn	*Baccharis halimifolia*	America
Autumn–spring	*Ageratum conyzoides*	America
Spring and summer	*Lantana camara*	Tropical America

* Produces a sugary honey dew when attacked by the fungus *Claviceps.*

species flourish with the rising temperature of that period. Although during 1952-1953 there was an unusually high rainfall in February, this is always the period of maximum rainfall; and although variations in the environment may occur from year to year affecting the *Drosophila* population to a greater or lesser extent, the general pattern of the succession described here is probably characteristic.

The majority of fruit-bearing plants in the area with which the *Drosophila* species may be associated (Table 4) fruit mainly in the summer and autumn; and although no positive information is available on the relationship of their fruit to the *Drosophila* species, it is significant that rotting fruits are abundant when the major peak of the *Drosophila* population does occur.

The only comparable survey to the present study is that conducted at Aldrich Farm, Austin, Texas, U.S.A. during July 1939-June 1940 (Patterson 1943), and it is of interest to compare the two (Table 5). It is possible that if the collection at Moggill had been as intensive as at Aldrich, additional species would have been collected, but at most these would have been rare, and, in fact, new records for the area.

At Moggill the subgenera *Pholadoris, Sophophora,* and *Drosophila* are represented, whereas at Aldrich the subgenera *Hirtodrosophila, Sophophora,* and *Drosophila* are present.

At Aldrich, *D. simulans* and *D. melanogaster,* of the *melanogaster* species group, are the abundant species, and reach their peak in autumn, following the maximum summer rains, thus accounting for the major peak of the whole *Drosophila* population for the year. At Moggill, where the maximum rainfall is also during the summer months, *D. simulans* and *D. serrata* (also of the *melanogaster* species group) behave in a similar fashion as described above. At Aldrich, as at Moggill, there are also species with their peak numbers in the spring, causing the minor spring peak in total numbers of the genus. There are also species which are more evenly distributed over the whole year.

TABLE 5
COMPARISON OF CONDITIONS AT MOGGILL AND ALDRICH FARMS

Observation	Moggill Farm	Aldrich Farm
Latitude	27.5°S.	31°N.
Distance from coast	17 miles	150 miles
Rainfall	41.40 in.	33.46 in.
Mean monthly temperature range	58.7-77.1°F	40.6-85.1°F
Specimens collected	7072	79,404
Species collected	16	25
Abundant species	2	2
Common species	7	10
Rare species	7	16

Six species, viz. *D. busckii, D. melanogaster, D. simulans, D. repleta, D. hydei,* and *D. immigrans* are common to both Moggill and Aldrich and it is of interest to compare the seasonal fluctuations of these species at the two localities. *D. busckii* is essentially a spring species at Aldrich and likewise at Moggill it is a late winter–early spring species. Due to *D. simulans* and *D. melanogaster* being treated as a complex at Aldrich, detailed comparisons cannot be made with these species, but from the data available, it is evident that whereas *D. melanogaster* is quite prevalent at Aldrich it is not so at Moggill. The closely related *D. hydei* and *D. repleta* are spring species both at Moggill and Aldrich. Finally, whereas *D. immigrans* does not show regular seasonal fluctuation at Aldrich, it is largely a late autumn–early winter species at Moggill.

D. versicolor is worthy of special discussion. This species has been assigned to the *mulleri* species group (Mather 1955) and a number of American members of this species group have been shown to breed on the fruit of species of cacti (Patterson 1943). It will be noted (Table 2) that the population peak of *D. versicolor* is in spring, whereas cacti species usually fruit in autumn. Further, no species of cacti were observed within

the collection area although it is possible that isolated specimens may grow within the vicinity of Moggill. It therefore seems possible that *D. versicolor* is not associated with cacti fruits in this area.

Thus the broad general picture at both Moggill and Aldrich is similar, the most outstanding difference at Moggill being the presence of six species belonging to the subgenus *Pholadoris* whereas at Aldrich no members of this subgenus are recorded.

V. Acknowledgments

Grateful acknowledgment is made to Professor W. Stephenson, Zoology Department, University of Queensland, for encouragement in this work; to Mr. B. W. Newmann, Queensland Meteorological Bureau, for climatic data; to Mr. A. B. Cribb, Botany Department, University of Queensland, for the flora survey of Moggill Farm; and Mr. M. Page, Zoology Department, University of Queensland, for assistance in the field work.

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Appendix I

Flora of Moggill Farm Collection Area

The area under investigation lies at the bottom of a gully running roughly north-east–south-west and flanked by slopes carrying open eucalypt forest. On the moister eastern aspect this forest comprises *Eucalyptus tereticornis* S. (blue gum) with a number of other species including *Tristania suaveolens* S. (swamp box), *E. tesselaris* F. Muell. (Moreton Bay ash), *Acacia aulacocarpa* A. Cunn., and *A. cunninghamii* Hook. On the drier western exposure *E. hemiphloia* F. Muell. (gum-top box) predominates with an occasional *E. maculata* Hook. (spotted gum). On both slopes there is a ground cover of grasses including *Bothriochloa decipiens* (Hack.) C. E. Hubb (pitted blue grass), *Cymbopogon refractus* (R. Br.) A. Camus (barb-wire grass), *Eragrostis leptostachya* Steud., and herbs

such as *Hydrocotyle* sp., *Oxalis corniculata* L., *Ionidium suffruticosum* Ging., *Glycine tabacina* Benth., and *Cheilanthes tenuifolia* Sw.

The comparatively flat floor of the gully is of very variable width, but often at least 80 ft across. At the junction of the gully flat and flanking slopes, a somewhat denser vegetation may appear in the moister habitat. With the blue gum and box appears *Casuarina glauca* Sieb. (swamp she-oak), while the scrambling *Lantana camara* L. is frequently well developed and a vigorous herbaceous ground cover appears in the protection of the tree cover. Amongst the grasses here are *Paspalum dilatatum* Poir., *Cynodon dactylon* Pers. (blue couch), *Oplismenus compositus* Beauv., and *Echinopogon nutans* C. E. Hubb, the latter two particularly in the more shaded positions. *Ageratum conyzoides* L. (billy goat weed) with its light blue inflorescence is extremely common, and amongst the other numerous herbaceous species are *Verbena officinalis* L., *Rumex* sp., *Commelina cyanea* R. Br., *Lobelia purpurascens* R. Br., and *Cyperus gracilis* R. Br. Herbaceous climbers such as *Passiflora suberosa* var. *minima* Jacq., *P. alba* L. & O., *Eustrephus latifolius* var. *angustifolia* Benth. are also frequently present.

Over the gully flat are a few trees of *Eucalyptus tereticornis* but the most common tree is *Casuarina glauca*. *Baccharis halimifolia* L. (groundsel) forms dense stands in places, particularly near the margins of the flat, and the spiny scrambling shrubs of *Cudrania javanensis* Trec. are scattered here and there. The ground cover is almost entirely of *Paspalum dilatatum* with *Cynodon dactylon* in places and a few herbs such as *Aster subulatus* Michx., *Oxalis corniculata*, and *Ageratum conyzoides*. In places, the flat is cut by a small stream and along its banks are developed some trees of *Callistemon viminalis* (Sol. ex Gaertn.) G. Don. ex Loud., *Melaleuca bracteata* F. Muell., and a few semi-rainforest species such as *Cryptocarya triplinervis* R. Br. and *Elaeocarpus obovatus* G. Don. Over these in many places is a dense layer of the climbing *Passiflora suberosa* var. *minima* and less frequently of *Ipomoea palmata* Forsk.

THE GENUS *DROSOPHILA* (DIPTERA) IN EASTERN QUEENSLAND

III. CYTOLOGICAL EVOLUTION

By W. B. MATHER*

(*Manuscript received July* 18, 1955)

Summary

The value of cytological methods in evolutionary studies, with particular reference to the genus *Drosophila,* is discussed.

The chromosomes of six species of the subgenus *Pholadoris* (*D. cancellata* Mather, *D. enigma* Mall., *D. lativittata* Mall., *D. novopaca* Mather, *D. novamaculosa* Mather, *D. bryani* Mall.), three species of the subgenus *Sophophora* (*D. serrata* Mall., *D. takahashii* Sturt., and *D. dispar* Mather), and one species of the subgenus *Drosophila* (*D. versicolor* Mather) are described and figured.

The cytological evolution of these species has been interpreted in terms of fusions, inversions, and addition of heterochromatin. The cytological picture of the species groups to which the Australian species belong is examined in relation to geographical distribution, and it is shown that these data are helpful in establishing the phylogeny of the subgenus *Pholadoris.*

I. INTRODUCTION

Within the genus *Drosophila* as a whole there is considerable chromosome diversity as shown in the metaphase plates of somatic mitoses, the number ranging from three pairs, e.g. *D. busckii* Coq. (Wharton 1943) to seven pairs, e.g. *D. trispina* Wheel. (Ward 1949). Also, the individual chromosomes may be in the form of rods, V's, J's, or dots depending on the position of the centromere and the length of the chromosome. However, within some sections of the genus, e.g. the *mulleri* subgroup consisting of 18 species, the chromosome configuration at metaphase is very constant (Patterson and Stone 1952). Throughout the genus, however, because of the presence of giant chromosomes in the larval salivary glands, with characteristic banding patterns, detailed analysis of chromosome differences can be made between species and within the strains of species. This leads to the establishment of phylogenetic relations in spite of constancy of metaphase plate configurations. This type of detailed analysis has been carried out in a number of species groups, e.g. *virilis* (Hsu 1952) and *mulleri* (Wasserman 1954).

In an earlier paper (Mather 1955) 10 Australian species of the genus *Drosophila* were described, and in the present paper a partial cytological analysis has been made of these species with the object of throwing light on their evolution.

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II. Methods

(*a*) *General*

Larvae for cytological purposes were grown on a standard medium (Spencer 1950), particular attention being paid to adequate nutrition by avoiding overcrowding and adding live yeast from time to time.

The technique of preparing larval brain and salivary gland squashes was based on that of Slizynski (1952) but it was found more convenient to dissect the larvae in 0.7 per cent. saline and to squash in 45 per cent. acetic acid. Staining in aceto-orcein (2 per cent. Gurr's synthetic orcein in 60 per cent. acetic acid*) was subsequently carried out by total immersion of the slide in the stain. Salivary glands were fixed for about 3 min in N HCl (Hsu 1952) before squashing in acetic acid to assist in spreading of the chromosome arms.

(*b*) *Sexing Larvae*

Although a knowledge of possible sex chromosome dimorphism was not essential for the purpose of this paper, an investigation of this was considered useful whilst the material was available. The best place, due to large cell size, in which to examine somatic metaphase chromosomes is in the neuroblast cells of the larval brain, and therefore, in order to detect sex chromosome dimorphism, either the larvae had to be sexed or sufficient used to ensure a high probability of sampling both males and females. Obviously the former is the more efficient method. Kerkis (1931) has shown that in *D. melanogaster* Meig. the males have considerably larger gonads than the females and this method was proved to be applicable to the present species by sexing the larvae, rearing, and checking their sex on emergence. Sexing was carried out by observing the gonads after gentle flattening between a cover slip and slide under a dissecting microscope, utilizing incident light against a black background.

(*c*) *Examination and Illustration*

Preparations were scanned for analysable figures under high power (for brains) and low power (for salivary glands) using a green filter. A disadvantage of the squash method for metaphase plates is that often the somatic pairing of homologous chromosomes is destroyed and the individual chromosomes distorted so that rods appear as V's and vice versa, bearing in mind that the centromeres often cannot be seen. Also the actual dimensions of the chromosomes may be distorted. For this reason the following procedure which is similar to that adopted by Clayton and Ward (1954) was used. Camera lucida drawings of metaphase plates were made using a $\times 100$ oil immersion objective and a $\times 20$ ocular. By an examination of these drawings, homologous chromosomes in each

* Synthetic orcein gives more intense staining than natural orcein (Dr. M. J. D. White, personal communication).

drawing and corresponding chromosomes in the series of drawings were determined for each species. The chromosome drawings were then measured and the mean length of each chromosome or chromosome arm

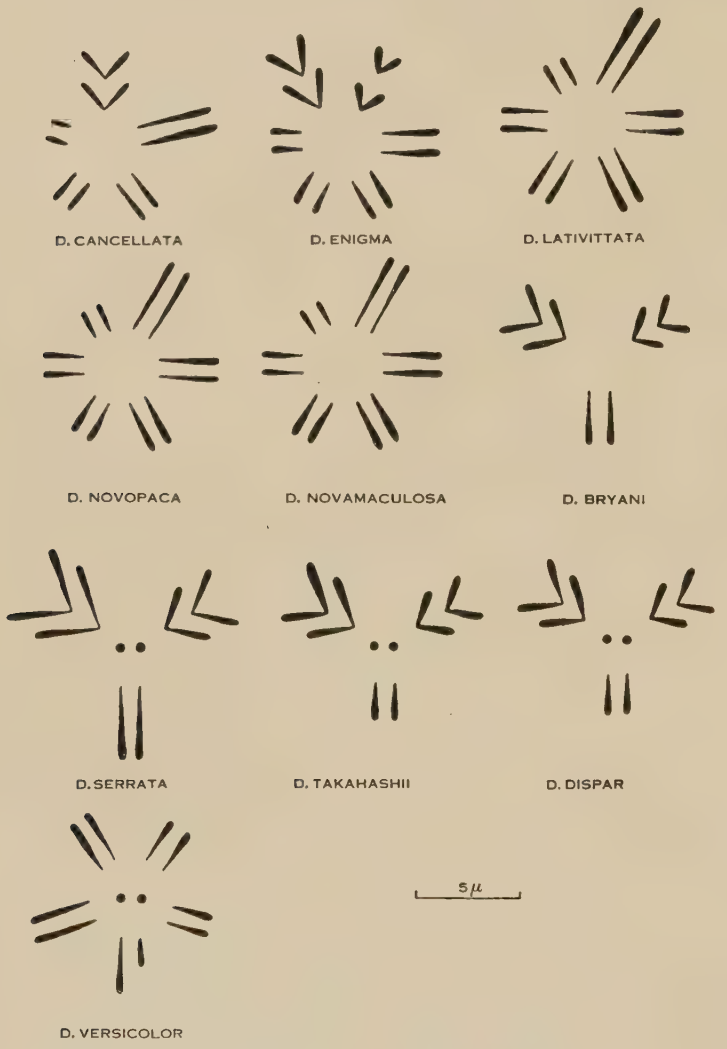

Fig. 1.—Composite drawings of metaphase plates.

determined. Finally, these data were used to prepare composite scale drawings (Fig. 1). With giant chromosome preparations, where it was only necessary to determine the number of arms, free-hand drawings were made.

III. Results

In Table 1 are set out the metaphase plates and salivary chromosome configurations of the species studied.

IV. Discussion

(*a*) *Theory of Chromosome Evolution*

Convincing evidence has been put forward that the primitive chromosome configuration for the genus *Drosophila* is five pairs of rods and one pair of dots (Sturtevant and Novitski 1941). The essence of their argument is that in many species where the chromosome configuration is other than five pairs of rods and a pair of dots, nevertheless six "elements" can be distinguished containing corresponding mutant genes.

Table 1

CHROMOSOME CONFIGURATIONS

L, long arm; *D*, dot chromosome

Species	Culture Source and Date	Haploid Chromosome No.	Salivary Chromosome Arms
D. cancellata	Moggill, Qld. 19.xi.1952	1 V, 4 rods	6 *L* + 1 *D*
D. enigma	Moggill, Qld. 28.v.1953	2 V's, 4 rods	5 *L*
D. lativittata	Moggill, Qld. 25.v.1952	6 rods	5 *L*
D. novopaca	Noosa, Qld. 9.i.1953	6 rods	5 *L* + 1 *D*
D. novamaculosa	Moggill, Qld. 19.xi.1952	6 rods	5 *L* + 1 *D*
D. bryani	Maroochydore, Qld. 26.ii.1955	2 V's, 1 rod	5 *L* + 1 *D*
D. serrata	Greenslopes, Qld. 4.vi.1952	2 V's, 1 rod, 1 dot	5 *L* + 1 *D*
D. takahashii	Samford, Qld. 22.vi.1952	2 V's, 1 rod, 1 dot	5 *L* + 1 *D*
D. dispar 1	Samford, Qld. 22.vi.1953	2 V's, 1 rod, 1 dot	
D. dispar 2	Binna Burra, Qld. 19.ii.1955	2 V's, 1 rod, 1 dot	5 *L* + 1 *D*
D. versicolor	Moggill, Qld. 23.xi.1952	5 rods, 1 dot	5 *L* + 1 *D*

It has been pointed out (Patterson and Stone 1952) that the simplest explanation of how this primitive chromosome configuration could change in the course of evolution to the other arrangements known is by way of chromosomal fusion with the elimination of a centromere, pericentric inversion (an inversion across the centromere), and the addition of heterochromatin to the original chromosome. There is also much greater likelihood of decrease in the centromere number than an increase. There have been only two occasions recorded where the centromere number increased above the primitive six pairs: in *D. fragilis* Wheel. and *D. trispina*, both with seven centromere pairs. In these cases it has been suggested that the "free" centromere released by a fusion has subsequently been established in the species. These changes would of course occur as single events and so originally would be in the heterozygous condition. However, they could become established in the homozygous condition in subsequent generations. Further, unless there is evidence to the contrary, it has been assumed that these changes have occurred in autosomes. In addition to pericentric inversions it is now known from a study of giant chromosomes that paracentric inversions (inversions not across the centromere) have been prevalent in *Drosophila* chromosomal evolution but these paracentric inversions do not become apparent in somatic metaphase

chromosomes. Paracentric inversions can only be detected by a detailed comparison of the banding pattern of the giant chromosomes or by detection of inversion loops in hybrid giant chromosome figures.

These chromosomal changes are useful in tracing phylogeny because the probability of exactly the same change occurring more than once is negligible.

The relationship of giant chromosomes to metaphase plates was established by Painter (1934), and the important fact made use of in this work is that heterochromatic chromosome arms of metaphase chromosomes do not show up in giant chromosomes but are aggregated in the chromocentre. Thus by studying giant chromosomes in relation to metaphase plates heterochromatic arms are detected. As an example of this relationship, *D. novopaca* Mather has a metaphase plate of six pairs of rods but a giant chromosome configuration of five long arms and one dot. This indicates that in the course of evolution heterochromatin has been added to the dot to produce a rod.

(*b*) *Subgenus* Pholadoris

The genus *Drosophila* has been divided into six subgenera (Sturtevant 1942) and in the present study the subgenera *Pholadoris, Sophophora,* and *Drosophila* are represented. The subgenus *Pholadoris* is of particular interest in this study because evidence has accumulated (Mather 1953, 1955; Harrison 1954) that there are many representatives of this subgenus in the Australian region. The limits of this and other biogeographical regions to be mentioned are those defined by Folsom and Wardle (1934). Mather (1955) has split the subgenus into (1) the *victoria* species group containing *D. lebanonensis* Wheel., *D. nitens* Buzzati., and *D. victoria* Sturt.; (2) the *coracina* group containing *D. cancellata* Mather, *D. coracina* Kikkawa & Peng, *D. enigma* Mall., *D. lativittata* Mall., and *D. novopaca*; (3) the *maculosa* group with one species *D. novamaculosa* Mather; (4) the *mirim* species group with *D. baeomyia* Wheel.* and *D. mirim* Dobz. & Pav.*; and (5) the *levis* group with only *D. bryani* Mall. Table 2 sets out the distribution of these species together with their metaphase plate and giant chromosome pictures. Centromere number and sex chromosome dimorphism are also listed. Finally, the fusions, pericentric inversions, and heterochromatin additions, which have been suggested as occurring in the evolution of these configurations, are listed. Four other species: *D. samoensis* Harrison, *D. marjoryae* Harrison, *D. excepta* Mall., and *D. anuda* Curran, all in the Australian region, have also been assigned to the subgenus *Pholadoris* but nothing is known about their chromosomes. The same applies to the 19 species recently assigned to the subgenus (Burla 1954*a*).

* Burla (1954*a*) has recently indicated that these species are synonymous with *D. latifasciaeformis* Duda.

(i) Maculosa *and* Coracina *Species Groups.*—The Australian species *D. novamaculosa, D. novopaca,* and *D. lativittata,* with metaphase plates of six pairs of rods and a centromere number of six pairs, are closest to the primitive condition of five pairs of rods and one pair of dots. The lengths of the chromosomes are also very similar (Fig. 1). As these species have a giant chromosome pattern of five long arms they have apparently evolved from the primitive condition by adding heterochromatin to the dot chromosome. The Australian species *D. enigma* is less primitive, the metaphase plates showing two pairs of V's and four pairs of rods and the giant chromosome picture showing five long arms, but the centromere number is still six pairs. This situation is most simply explained by assuming that heterochromatin has been added to two of the autosomes and to the dot chromosome. *D cancellata,* also an Australian species, is still less primitive with a metaphase plate of one pair of V's and four pairs of rods and a giant chromosome pattern of six long arms and one dot. Here the centromere number is reduced for the first time to five pairs, and the most simple explanation is that there has been a fusion of an autosome to a dot chromosome and a pericentric inversion in an autosome.

Passing to the Oriental and Palaearctic species *D. coracina,* there is a metaphase plate of one pair of rods, two pairs of V's, and one pair of dots. This is the only member of the *coracina* group outside Australia, and, although the details of its cytological evolution cannot be deduced until its giant chromosomes are reported on, from its metaphase plate it is obvious that extensive changes have occurred in evolving from the primitive condition, and its centromere number of four pairs is less than the other members of the group. Therefore, cytologically, it is most advanced of the species considered so far.

(ii) Victoria *Species Group.*—No members of the *victoria* species group have been recorded from Australia. The Palaearctic *D. lebanonensis* and the Nearctic *D. victoria* both have a metaphase plate of one pair of rods, two pairs of large V's, and one pair of small V's. Their salivary chromosome pattern consists of six long arms and one dot. The deduction can therefore be made that in evolving from the primitive condition there was a fusion of two autosomes, a fusion of an autosome to a dot, a pericentric inversion of an autosome, and the addition of heterochromatin to the dot chromosome. *D. nitens,* the third member of the *victoria* group, is a Palaearctic species with a metaphase plate of four pairs of V's and hence has a centromere number of four pairs. The giant chromosome picture has not been studied, but from the metaphase plates obviously extensive changes have occurred in evolving from the primitive condition. Thus all members of the *victoria* group are more advanced cytologically than the majority of the *coracina* group.

(iii) Mirim *Species Group.*—The *mirim* species group consists of the Neotropical species *D. baeomyia* and the Nearctic species *D. mirim* both

with a metaphase plate of three pairs of V's and consequently a centromere number of three pairs. The giant chromosome configuration consists of six long arms. No suggestions as to the ways in which this has come about are made by the authors, but from the data available it can be deduced that two autosomes fused on two occasions, the dot chromosome fused to an autosome, and subsequently this compound chromosome underwent a pericentric inversion.

(iv) Levis *Species Group.*—The Australian *levis* species group with one species, *D. bryani,* is closely related morphologically to the *mirim* group. With a metaphase plate of one pair of rods and two pairs of V's it has a centromere number of three pairs. In the giant chromosome configuration there are five long arms and a dot, and apparently here two pairs of autosomes fused, and the dot fused to an autosome. Hence, although *D. baeomyia, D. mirim,* and *D. bryani* all have a centromere number of three pairs, *D. bryani* is slightly more primitive cytologically than the other two.

(v) *Relationship of Species Groups.*—That the subgenus *Pholadoris* is old is indicated by the fact that it occurs scattered over the world and that it contains members with a primitive chromosome configuration. Thus the subgenus apparently split off from the ancestral *Drosophila* stock before fusions and pericentric inversions had occurred. Due to lack of fossil evidence it is impossible to be sure in what part of the world the genus *Drosophila* or the subgenus *Pholadoris* arose, but on present day distribution of morphologically primitive species (Patterson and Stone 1952) it seems likely that the genus arose in the eastern Palaearctic. If this is true the subgenus *Pholadoris* probably also originated here and radiated out in several directions (Fig. 2). From the centre a line of evolution gave rise to the *coracina* species group with *D. coracina* in the Palaearctic region and *D. novopaca, D. lativittata,* and *D. enigma* in the Australian region. The cytology of *D. cancellata* indicates that it split off the main *coracina* line before *D. novopaca, D. lativittata,* and *D. enigma.*

D. novamaculosa, although cytologically similar to *D. novopaca* and *D. lativittata,* differs in certain important phenotypic characters and apparently split off as a species group from the main *coracina* line in the Australian region.

The line comprising the *victoria* species group gave *D. nitens* in the Palaearctic region and *D. victoria* in the Nearctic region. *D. lebanonensis* from the Palaearctic region freely interbreeds with *D. victoria* and it has been suggested that these species are identical (Buzzati-Traverso and Scossiroli 1952).

The cytological configurations of *D. mirim* and *D. baeomyia,* members of the *mirim* species group in the Nearctic and Neotropical regions respectively, are such that they could not have been evolved from *D. victoria.* As the Australian *levis* group is morphologically closely related to the *mirim* group, and has a metaphase configuration differing only in

the lack of an autosomal pericentric inversion, it seems possible that these two species groups had a common origin somewhere in the Palaearctic region, the *mirim* group migrating to the Nearctic and Neotropical regions, and the *levis* group migrating into the Australian region.

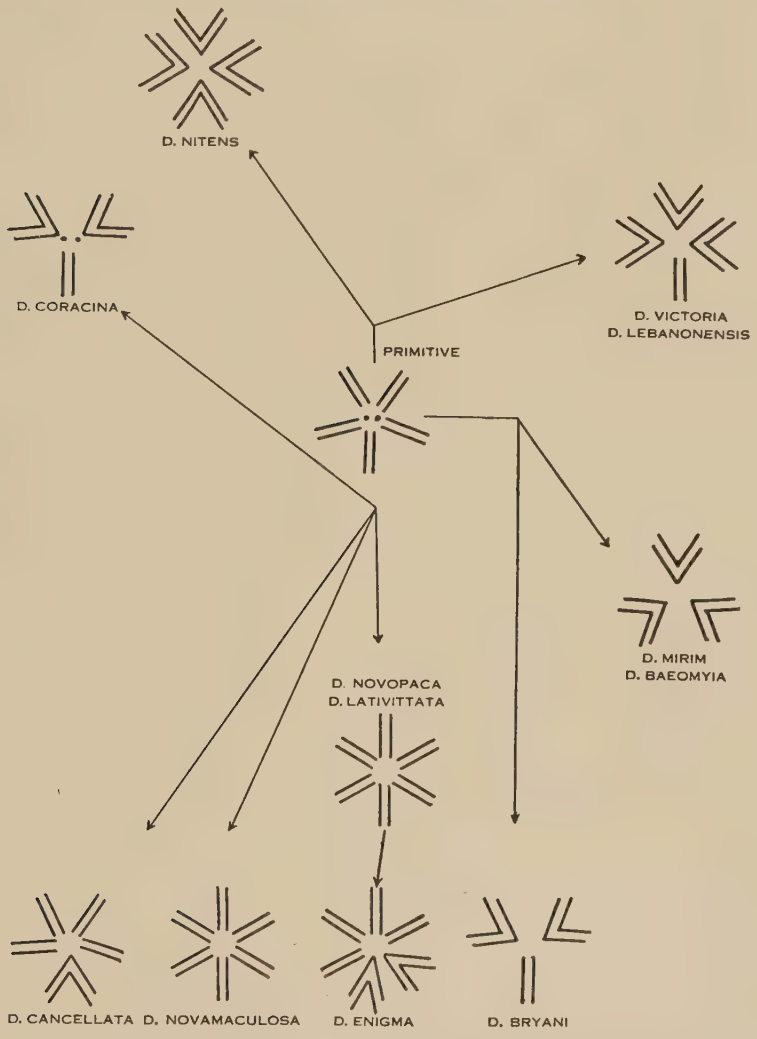

Fig. 2.—Subgenus *Pholadoris* — relationships. (Metaphase plates, diagrammatic).

Perhaps the most interesting feature brought to light by the present study is that Australia is a region containing a number of cytologically primitive members of the *Pholadoris* subgenus, perhaps representing a relict fauna.

It will be noted from Table 2 that only in *D. lebanonensis* has sex chromosome dimorphism been reported. Also in *D. enigma* and *D.*

TABLE 2

CYTOLOGICAL ANALYSIS OF THE SUBGENUS PHOLADORIS

A = Autosome, *D* = dot chromosome, *L* = long arm, *R* = long rod, *r* = short rod, *V* = large V, *v* = small V, *X* = *X*-chromosome, *Y* = *Y*-chromosome, brackets = deduction made by author. Palae. = Palaearctic, Near. = Nearctic, Aust. = Australia, Ori. = Oriental, Neotr. = Neotropical

Species Group	Species	Distribution	Metaphase Plate Haploid	Centromeres Haploid	Salivary Gland Config.	Authority	Derivation from 5 Rods, 1 Dot, Metaphase Plate									Sex Chromosome Dimorphism
							Fusions				Pericentric Inversions			Heterochromatin Additions			
							X-A	*X-D*	*A-A*	*A-D*	*X*	*A*	*D*	*X*	*A*	*D*	*X Y*
victoria	*D. lebanonensis*	Palae.	1*R*, 2*V*, 1*v*	4	6*L*, 1*D*	Ward 1949			1	1		1				1	*R r*
	D. nitens	Palae.	4*V*	4	?	Buzzati-Traverso 1943				?		?				?	
	D. victoria	Near.	1*R*, 2*V*, 1*v*	4	6*L*, 1*D*	Wharton 1943			1	1		1				1	
coracina	*D. cancellata*	Aust.	4*R*, 1*V*	5	6*L*, 1*D*	Author				1		1					
	D. coracina	Palae. and Ori.	1*R*, 2*V*, 1*D*	4	?	Kikkawa & Peng 1938				?		?			?		
	D. enigma	Aust.	4*R*, 2*V*	6	5*L*	Author									2	1	
	D. lativittata	Aust.	6*R*	6	5*L*	Author										1	
	D. novopaca	Aust.	6*R*	6	5*L*, 1*D*	Author										1	
maculosa	*D. novamaculosa*	Aust.	6*R*	6	5*L*, 1*D*	Author										1	
mirim	*D. baeomyia*	Neotr.	3*V*	3	6*L*	Clayton & Ward 1954			(2)	(1)		(1)					
	D. mirim	Near.	3*V*	3	6*L*	Dobzhansky & Pavan 1943			(2)	(1)		(1)					
levis	*D. bryani*	Aust.	1*R*, 2*V*	3	5*L*, 1*D*	Author			2	1							

lativittata the dot chromosome cannot be detected in the giant chromosome preparations. No explanation can be given on this point although it has been reported without explanation in other species, e.g. *D. baeomyia* and *D. mirim.*

(*c*) *Subgenus* Sophophora: Melanogaster *Species Group*

(i) Montium *Subgroup.*—On morphological grounds, *D. serrata* has been placed in the *montium* subgroup of the *melanogaster* species group (Mather 1955) which contains in addition *D. auraria* Peng, *D. ficusphila* Kikkawa & Peng, *D. kikkawa* Burla,* *D. montium* de Meijere,* *D. nipponica* Kikkawa & Peng, and *D. rufa* Kikkawa & Peng (Table 3). *D. serrata* has a metaphase plate of one pair of rods, two pairs of V's, and one pair of dots, and hence four pairs of centromeres. The salivary gland picture has five long arms and one dot and hence the chromosomes have evolved from the primitive condition by the fusion of two pairs of autosomes. The metaphase plates of *D. rufa, D. ficusphila,* and *D. auraria* are similar to *D. serrata,* but as the giant chromosomes have not been examined, evolutionary changes of the chromosomes cannot be deduced. Three strains of *D. kikkawa* have been examined cytologically, and all three have a giant chromosome configuration of five long arms and one dot and four pairs of centromeres. In two strains the metaphase plates consist of two pairs of rods and two pairs of V's, having apparently evolved by the fusion of two pairs of autosomes and the acquisition of heterochromatin by the dot. The third strain has a metaphase plate of one pair of rods, two pairs of large V's, and one pair of small V's, indicating that there has been fusion of two pairs of rods and addition of heterochromatin to the dot, as above, and a subsequent pericentric inversion in this chromosome. Sex chromosome dimorphism was not detected in *D. serrata,* and it is in this respect like *D. rufa.* However, in *D. auraria, D. ficusphila,* and *D. kikkawa* (strain 1), the *Y*-chromosome is a shorter rod than the *X,* and in *D. kikkawa* (strains 2 and 3) the *Y*-chromosome is a small V.

(ii) Takahashii *Subgroup.*—*D. lutea* Kikkawa & Peng and *D. takahashii* Sturt., constitute the *takahashii* subgroup of the *melanogaster* species group and, in this study, a new strain of *D. takahashii* has been cytologically examined. The metaphase plates show one pair of rods, two pairs of V's, and one pair of dots and hence four pairs of centromeres. The giant chromosomes show five long arms and one dot indicating a fusion of two pairs of autosomes during evolution. *D takahashii* (strain 1) is similar, but in *D. takahashii* (strain 2), although having a similar giant chromosome pattern, a metaphase plate of one pair of J's and two pairs of V's indicates a fusion of the *X*-chromosome with the dot in addition to the above changes. *D. lutea* has a metaphase plate of one pair of rods, two pairs of V's, and one pair of dots, but, as the giant chromosomes are

* Burla (1954*b*) has pointed out that what has been called *D. montium* does not correspond to the type of the species and he has renamed "*D. montium*", *D. kikkawa.*

TABLE 3

CYTOLOGICAL ANALYSIS OF MONTIUM AND TAKAHASHII SUBGROUPS

A = Autosome, D = dot chromosome, L = long arm, R = long rod, r = short rod, V = large V, v = small V, X = X-chromosome, Y = Y-chromosome, J = J-chromosome, Palae. = Palaearctic, Ori. = Oriental, Neotr. = Neotropical, Aust. = Australia

Species Group	Species	Distribution	Metaphase Plate Haploid	Centromeres Haploid	Salivary Gland Config.	Authority	Derivation from 5 Rods, 1 Dot, Metaphase Plate: Fusions X-A	Fusions X-D	Fusions A-A	Fusions A-D	Pericentric Inversions X	Pericentric Inversions A	Pericentric Inversions D	Heterochromatin Additions X	Heterochromatin Additions A	Heterochromatin Additions D	Sex Chromosome Dimorphism X Y
montium	*D. auraria*	Palae. and Ori.	1*R*, 2*V*, 1*D*	4	?	Kikkawa & Peng 1938		?				?				?	*R r*
	D. ficusphila	Palae.	1*R*, 2*V*, 1*D*	4	?	Kikkawa & Peng 1938		?				?				?	*R r*
	*D. kikkawa 1**	Neotr., Palae., Ori., and Aust.	2*R*, 2*V*	4	5*L*, 1*D*	Ward 1949			2							1	*R r*
	D. kikkawa 2	Neotr., Palae., Ori., and Aust.	2*R*, 2*V*	4	5*L*, 1*D*	Kikkawa 1936			2							1	*R v*
	D. kikkawa 3	Neotr., Palae., Ori., and Aust.	1*R*, 2*V*, 1*v*	4	5*L*, 1*D*	Kikkawa 1936			2				1			1	*R v*
	D. nipponica	Palae.	?	?	?			?				?				?	?
	D. rufa	Palae.	1*R*, 2*V*, 1*D*	4	?	Kikkawa & Peng 1938		?				?				?	
	D. serrata	Aust.	1*R*, 2*V*, 1*D*	4	5*L*, 1*D*	Author			2								
takahashii	*D. lutea*	Palae.	1*R*, 2*V*, 1*D*	4	?	Kikkawa & Peng 1938		?				?				?	*R r*
	D. takahashii 1	Palae., Ori., and Aust.	1*R*, 2*V*, 1*D*	4	5*L*, 1*D*	Ward 1949			2								*R r*
	D. takahashii 2	Palae., Ori., and Aust.	1*J*, 2*V*	4	5*L*, 1*D*	Sturtevant 1942	1		2								*J r*
	D. takahashii 3	Palae., Ori., and Aust.	1*R*, 2*V*, 1*D*	4	5*L*, 1*D*	Author			2								

* "*D. montium*" has been renamed *D. kikkawa* (Burla 1954*b*).

unknown, no deductions about the cytological evolution of this species can be made except that the centromere number is reduced from six to four pairs. In the strain of *D. takahashii* studied here no sex chromosome dimorphism was detected although in *D. lutea* and *D. takahashii* (strain 1) the *Y*-chromosome is a smaller rod than the *X*, and in *D. takahashii* (strain 2) the *X*-chromosome is a J and the *Y* a small rod.

TABLE 4

CYTOLOGICAL ANALYSIS OF MULLERI SUBGROUP

A = Autosome, *D* = dot chromosome, *L* = long arm, *R* = large rod, *r* = small rod, *V* = large V, *v* = small V, *X* = *X*-chromosome, *Y* = *Y*-chromosome, *J* = *J*-chromosome, Near. = Nearctic, Neotr. = Neotropical, Palae. = Palaearctic, Aust. = Australia

Species	Distribution	Metaphase Plate Haploid	Centromeres Haploid	Salivary Gland Config.	Authority	Heterochromatin Additions	Sex Chromosome Dimorphism *X Y*
D. aldrichi	Near. and Neotr.	5*R*, 1*D*	6	5*L*, 1*D*	Wharton 1943		*R r*
D. anceps	Near.	6*R*	6	5*L*, 1*D*	Patt. & Main. 1944	1*D*	*R r*
D. arizonensis	Near.	5*R*, 1*D*	6	5*L*, 1*D*	Wharton 1943		*R r*
D. buzzatii	Neotr. and Palae.	5*R*, 1*D*	6	5*L*, 1*D*	Wharton 1943		*R r*
D. hamatofila	Near. and Neotr.	5*R*, 1*D*	6	5*L*, 1*D*	Wharton 1943		*R r*
D. hexastigma	Near.	5*R*, 1*D*	6	5*L*, 1*D*	Patt. & Main. 1944		*R v*
D. longicornis	Near. and Neotr.	5*R*, 1*D*	6	5*L*, 1*D*	Wharton 1943		*R J*
D. mainlandi	Near.		?	?		?	?
D. meridiana	Near.	5*R*, 1*D*	6	5*L*, 1*D*	Wharton 1943		*R r*
D. mojavensis	Near.	5*R*, 1*D*	6	5*L*, 1*D*	Wharton 1943		*R r*
D. mulleri	Near. and Neotr.	5*R*, 1*D*	6	5*L*, 1*D*	Wharton 1943		*R r*
D. peninsularis	Near.	5*R*, 1*D*	6	5*L*, 1*D*	Wharton 1943		*R r*
D. racemova	Near. and Neotr.	5*R*, 1*D*	6	5*L*, 1*D*	Patt. & Main. 1944		*R v*
D. ritae	Near. and Neotr.	5*R*, 1*D*	6	5*L*, 1*D*	Wharton 1943		
D. spenceri	Near.	?	?	?		?	?
D. subviridis	Near.	?	?	?		?	?
D. stalkeri	Near.	5*R*, 1*D*	6	5*L*, 1*D*	Clayton & Ward 1954		*R J*
D. versicolor	Aust.	5*R*, 1*D*	6	5*L*, 1*D*	Author		*R r*
D. wheeleri	Near.	5*R*, 1*D*	6	5*L*, 1*D*	Clayton & Ward 1954		*R r*

Thus in these two species subgroups there is a constant centromere number of four pairs and similar changes have gone on in evolving from the primitive chromosome pattern, precluding any suggestion of deducing phylogenetic relationship without recourse to detailed studies of banding pattern in the giant chromosomes.

(iii) Dispar *Species Group.*—*D. dispar* has been placed in the *dispar* species group on morphological grounds (Mather 1955). It has a metaphase plate of one pair of rods, two pairs of V's, and one pair of dots, giving a centromere number of four pairs. In giant chromosome preparations there are five long arms and one dot indicating the fusion of two pairs of autosomes. Present knowledge of the cytology is therefore not helpful in detecting its phylogeny.

(*d*) *Subgenus* Drosophila: Repleta *Species Group*

(i) Mulleri *Subgroup*.—On morphological grounds *D. versicolor* was placed in the *mulleri* subgroup of the *repleta* species group (Mather 1955) (Table 4). It has a metaphase plate of five pairs of rods and one pair of dots. The giant chromosomes show five long arms and one dot. Therefore no cytological changes have occurred in its evolution from the primitive pattern, with the probable exception of paracentric inversions. All members of the *mulleri* subgroup whose chromosomes have been studied have this pattern, except *D. anceps* Patt. & Main. which has six pairs of rods in the metaphase plate and giant chromosomes like the other members of the group, indicating the addition of heterochromatin to the dot chromosome. The chromosome pictures of *D. mainlandi* Patt., *D. spenceri* Patt., and *D. subviridis* Patt. & Main. are not known. In *D. versicolor* the *Y*-chromosome is a shorter rod than the *X*, and this is the common pattern through the species group, except for *D. hamatophila* Patt. & Wheel. and *D. peninsularis* Patt. & Wheel. where the *Y-chromosome* is a small V and the *X* a rod, and *D. hexastigma* Patt. & Main. and *D. stalkeri* Wheel. where the *Y*-chromosome is a J and the *X* a rod. The Australian species *D. versicolor* is the only member of the *mulleri* subgroup outside the Neotropical and Nearctic regions, although *D. mercatorum* Patt. & Wheel. of the closely related *mercatorum* subgroup has been found in Honolulu (Patterson and Wheeler 1942).

Thus, in the *mulleri* group, very little cytological evolution involving fusions, pericentric inversions, and addition of heterochromatin has occurred which would be helpful in elucidating phylogenetic relationships. However, it has been shown (Wasserman 1954) that paracentric inversions have occurred extensively in this subgroup and by an analysis of these, phylogenetic relations have been worked out.

V. Acknowledgments

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THE GENUS *DROSOPHILA* (DIPTERA) IN EASTERN QUEENSLAND

IV. THE HYBRIDIZATION RELATIONSHIPS OF FOUR SPECIES OF THE PHOLADORIS SUBGENUS

By W. B. MATHER*

(*Manuscript received November* 3, 1955)

Summary

Hybridization tests have shown that four Australian morphospecies of the subgenus *Pholadoris*, genus *Drosophila* (*D. novopaca* Mather, *D. cancellata* Mather, *D. lativittata* Mall., and *D. enigma* Mall.), are biospecies, but that the following combinations yield adult offspring: *D. novopaca* × *D. lativittata* both ways, *D. novopaca* × *D. cancellata* both ways, ♂ *D. novopaca* × ♀ *D. enigma*, and ♂ *D. cancellata* × ♀ *D. lativittata*, and that "gene exchange" is possible between *D. cancellata* and *D. novopaca* under laboratory conditions.

Sexual isolation, hybrid inviability, and hybrid sterility all play a part in keeping the species distinct from one another.

The results of the hybridization tests support the hypothesis that the species should be placed in one species group (*coracina*) as was previously done on morphological criteria.

Of the three main morphological characters used for separating these species, viz. thoracic, abdominal, and wing markings, those of *D. novopaca* are dominant to those of *D. cancellata*. These character differences between at least *D. novopaca* and *D. cancellata* seem to be controlled by one sex-linked gene.

I. INTRODUCTION

The *coracina* species group (Mather 1955) comprising the Palaearctic and Oriental species *Drosophila coracina* Kikkawa & Peng, and the Australian species *D. cancellata* Mather, *D. enigma* Mall., *D. lativittata* Mall., and *D. novopaca* Mather was erected on purely morphological criteria. Hence these species were morphospecies but not necessarily biospecies in the sense recently developed by Cain (1954).

It has been shown that the Australian members of this group are sympatric in at least part of their range (Mather 1956*a*) and therefore there is no indication that geographic isolation is effective today in acting as an isolating mechanism. Because of this it was decided to determine, by attempted hybridization (i) if these four morphospecies were in fact biospecies, (ii) if so, what parts sexual isolation, hybrid inviability, and hybrid sterility play in keeping them as biospecies, and (iii) if there is biological evidence for placing these species in one group. Although this approach has been extensively used in recent years for other species groups of the genus (Patterson and Stone 1952) it has not previously been applied to the subgenus *Pholadoris*.

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The outstanding morphological differences between the species under consideration are thoracic pattern, abdominal markings, and presence or absence of clouding over the wing crossveins (Mather 1955). *D. novopaca* has a plain black thorax and abdominal segments whereas the others have striped thoraces and abdominal segments marked with yellow in characteristic ways. *D. cancellata* alone of the four has clouding over the wing crossveins. Therefore, if any hybrids could be produced, these might be useful in analysing the genetics of these differences. In addition, the appearance of hybrid giant chromosomes would also possibly be helpful in deciding the taxonomic rank of the four species.

II. Materials and Methods

Cultures were started from females fertilized in the wild as follows: *D. cancellata* (Moggill, 19.xi.1952), *D. enigma* (Moggill, 28.v.1953), *D. lativittata* (Moggill, 25.v.1952), and *D. novopaca* (Noosa, 9.i.1953) (Mather 1955). From the above cultures all virgin flies were collected every 24 hr, sorted into sexes, and 8 to 12 individuals of each sex placed in 3 × 1 in. culture vials to mature for 5-9 days. The 12 possible interspecific crosses were then attempted by placing approximately 10 pairs of flies in culture tubes.

The tubes were checked for larvae after 1 week, and the flies transferred to new medium. This was repeated until the experiment had run for 1 month. Each culture was re-checked for larvae 1 week after removal of the flies in order to detect fertilized eggs laid immediately before the transference of the flies. Vials containing larvae were kept for 4 weeks longer and examined for adults or pupae. Each cross was replicated 10 times.

The tests were carried out on standard medium (Spencer 1950) in an air-conditioned room at a temperature of 22.5 ± 1°C. Controls were not run for these tests because during previous investigation of these species (Mather 1956*b*) under identical experimental conditions it was found that in intraspecific matings as few as three pairs of flies per vial always produced viable offspring.

The same general procedure was used in attempting to breed to the F_2 generation, or backcrossing the F_1 generation to either of the parents.

Tests for sexual isolation were made by examining the genital tracts of a sample of females which had been exposed to males for four weeks and determining if sperm were present.

Hybrid sterility was investigated by examining the ovaries of a sample of females which had matured for 5 weeks without laying eggs. Slides of hybrid salivary gland giant chromosomes were prepared by a standard method (Mather 1956*b*).

TABLE 1

P_1 CROSSES

I = Extreme intersex (Wharton 1942); A = abnormal abdomen

Attempted Cross	Fertile Vials	Progeny ♀	Progeny ♂	Parental Resemblances: Thorax Pattern	Parental Resemblances: Abdomen Pattern	Parental Resemblances: Clouding over Crossveins	Sexual Isolation*	Hybrid Inviability ♀	Hybrid Inviability ♂	Hybrid Sterility‡
lativittata ♂ × *novopaca* ♀	3/10	14		*novopaca*	*novopaca*†	*novopaca*			?	
lativittata ♀ × *novopaca* ♂§	9/10	165 + 34I		*novopaca*	*novopaca*†	*novopaca*			+	+(6/6)
cancellata ♂ × *enigma* ♀	0/10						+(13/13)			
cancellata ♀ × *enigma* ♂	0/10						+(29/29)			
cancellata ♂ × *lativittata* ♀	2/10	2		*lativittata*	*lativittata*	*lativittata*†			?	
cancellata ♀ × *lativittata* ♂	0/10						+(16/17)			
cancellata ♂ × *novopaca* ♀	5/10	8	1	*novopaca*	*novopaca*†	*novopaca*†				
cancellata ♀ × *novopaca* ♂§	9/10	28 + 7A	9	*novopaca* *cancellata*	*novopaca*† *cancellata*	*novopaca*† *cancellata*				
enigma ♂ × *lativittata* ♀	0/10						+(17/17)			
enigma ♀ × *lativittata* ♂	2/10	12 pupae						+		
enigma ♂ × *novopaca* ♀	0/10						+(26/26)			
enigma ♀ × *novopaca* ♂	2/10	18 + 3A		*novopaca*	*novopaca*†	*novopaca*			+	+(2/2)

* Figures in brackets are the fraction of females dissected which did not show sperm in their reproductive tract after exposure to males for 1 month.

† Not fully expressed.

‡ Figures in brackets are the fraction of females dissected which showed degenerate ovaries and no eggs in the vials after maturing for 5 weeks.

§ Giant chromosome pairing was poor.

III. Results

(*a*) P_1 *Crosses* (*Table 1*)

Of the attempted P_1 crosses, *D. novopaca* can be crossed to *D. lativittata* and *D. novopaca* to *D. cancellata* both ways, ♂ *D. novopaca* to ♀ *D. enigma,* and ♂ *D. cancellata* to ♀ *D. lativittata,* all with the production of viable adults. Also ♂ *D. lativittata* can be crossed to ♀ *D. enigma* to the extent of producing pupae but not adults.

In all crosses producing adult progeny the number of individuals produced per vial is very low compared with intraspecific matings where some hundreds of individuals are produced. Also in most successful crosses no males were produced, and even in the cross *D. cancellata* × *D. novopaca* where they did occur they were far outnumbered by females.

In the hybrids involving *D. novopaca* its characters are usually present but not completely expressed as regards abdominal pattern and clouding over crossveins. Thus the completely black abdominal pattern of *D. novopaca* is slightly indented dorsally with yellow on the 2nd-4th segments when *D. novopaca* is crossed with any of the other three species. Also there is slight clouding over the crossveins when *D. novopaca* is crossed with *D. cancellata.*

The only exception to the domination of *D. novopaca* characters has been in the nine males of the ♂ *D. novopaca* × ♀ *D. cancellata* cross which all had *D. cancellata*-like characters.

When ♀ *D. lativittata* is crossed to ♂ *D. cancellata, D. lativittata* characters are dominant but there is slight clouding over the crossveins.

As regards isolating mechanisms, there is clear-cut evidence of considerable sexual isolation between the species that do not hybridize: *D. cancellata* × *D. enigma* both ways, ♂ *D. enigma* × ♀ *D. lativittata,* and ♂ *D. enigma* × ♀ *D. novopaca.* At least some hybrid inviability of the males exists in some of the fertile crosses and of both males and females in the ♀ *D. enigma* × ♂ *D. lativittata* cross. In the crosses ♀ *D. lativitatta* × ♂ *D. novopaca* and ♀ *D. enigma* × ♂ *D. novopaca,* probably some hybrid sterility exists in the females. Where sufficient material was available, viz. in the ♀ *D. lativittata* × ♂ *D. novopaca* cross and in the ♀ *D. cancellata* × ♂ *D. novopaca* cross, the hybrid salivary gland chromosomes were examined, and in each case failure of pairing over extensive regions was found.

(*b*) $F_1 \times P_1$ *and* $F_1 \times F_1$ *Crosses* (*Table 2*)

In those cases where a reasonable number of progeny (more than 16) were obtained in the F_1, $F_1 \times P_1$ and $F_1 \times F_1$ crosses have been attempted. In the case of the ♀ *D. cancellata* × ♂ *D. novopaca* cross it was possible to backcross the females produced to either ♂ *D. cancellata* or ♂ *D. novopaca* with the production of viable offspring. As in the P_1 crosses,

TABLE 2

$F_1 \times P_1$ AND $F_1 \times F_1$ CROSSES : A = ABNORMAL ABDOMEN

Attempted Cross	Fertile Vials	Progeny ♀	Progeny ♂	Thorax	Abdomen	Clouding over Crossveins	Sexual Isolation*
(*lativittata* ♀ × *novopaca* ♂) ♀ × *lativittata* ♂	0/3						—(5/5)
(*lativittata* ♀ × *novopaca* ♂) ♀ × *novopaca* ♂	0/3						—(1/1)
(*cancellata* ♀ × *novopaca* ♂) ♀ × *cancellata* ♂	4/6	10 9	2	*novopaca* *cancellata*	*novopaca*† *cancellata*	*novopaca*† *cancellata*	
(*cancellata* ♀ × *novopaca* ♂) ♀ × *novopaca* ♂	1/1	1+2A	2	*novopaca*	*novopaca*	*novopaca*	
(*enigma* ♀ × *novopaca* ♂) ♀ × *enigma* ♂	0/1						
(*enigma* ♀ × *novopaca* ♂) ♀ × *novopaca* ♂	0/1						—(2/2)
(*cancellata* ♀ × *novopaca* ♂) ♀ × (*cancellata* ♀ × *novopaca* ♂) ♂	0/1						

* Figures in brackets are the fraction of females dissected which showed sperm in their reproductive tract after exposure to males for 1 month.

† Not fully expressed.

females heavily outnumbered males. In the former cross, 10 individuals were produced with *D. novopaca* characters, which were, however, not fully expressed as regards the abdomen and clouding over the crossveins, and 11 individuals with *D. cancellata* characters. In the latter cross, individuals with fully expressed *D. novopaca* characters were produced.

As regards isolating mechanisms in these crosses, sexual isolation was the only one considered, and it was not found in the crosses: hybrid (♀ *D. lativittata* × ♂ *D. novopaca*) × ♂ *D. lativittata,* hybrid (♀ *D. lativittata* × ♂ *D. novopaca*) × ♂ *D. novopaca,* and hybrid (♀ *D. enigma* × ♂ *D. novopaca*) × ♂ *D. novopaca.* However, only small numbers were examined.

IV. Discussion

(*a*) *Taxonomic Status of Hybridizing "Species"*

As "gene exchange" has been demonstrated between *D. novopaca* and *D. cancellata,* the question arises whether here there is one biospecies exhibiting polymorphism or two distinct biospecies. Although hybridization is relatively easy between these two morphospecies the number of individuals produced per vial is strikingly less than in a comparable intraspecific mating. Also the heterozygous sex (males) is markedly deficient in number, which is a characteristic of hybrids (Haldane 1922; Dobzhansky 1937). Cytologically the hybrid salivary gland chromosomes show poor pairing indicating considerable detailed chromosome differences between these morphospecies. Thus, present evidence indicates that sufficient isolating mechanisms have developed between these two morphospecies for them to be ranked as biospecies.

Gene exchange has not been demonstrated between the progeny of the other P_1 crosses which produced offspring but may have been if more material had been available. However, on the evidence, the same arguments as above would apply and hence it may be concluded that the four morphospecies are in fact biospecies.

(*b*) *Phylogeny of Species*

Despite the species being biospecies they nevertheless bear a close phylogenetic relationship to one another since they are linked together by a chain of hybridization (Fig. 1), and there is biological justification for placing them in one species group as they were originally on morphological criteria (Mather 1955). Thus the evidence from this work is not at variance with the phylogenetic tree postulated on cytological evidence (Mather 1956*b*). However, because strong isolating mechanisms may be developed between phylogenetically closely related species the evidence from this work adds nothing to the exact placing of species on a phylogenetic tree.

(c) *Genetics of Species Differences*

With the exception of the ♀ *D. cancellata* × ♂ *D. novopaca* cross, the appearance of the F_1 progeny when *D. novopaca* is involved in a cross clearly indicate that as regards thoracic, abdominal, and wing markings, its characters are being expressed, leading to the conclusion that the gene or genes controlling these characters in *D. novopaca* are dominant to those in the other three species. Likewise, the gene or genes controlling these characters in *D. lativittata* are dominant to those in *D. cancellata.*

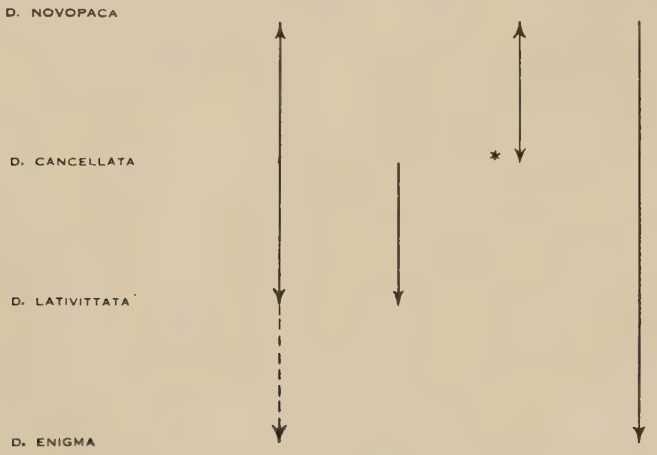

Fig. 1.—Hybridization relationships. Arrowheads indicate ♂ to ♀ cross. ----- Pupae only. * Indicates the only cross in which breeding past the F_1 generation was possible.

However, in the case of ♂ *D. novopaca* × ♀ *D. cancellata* cross the gene or genes responsible for the above characters are sex-linked since males differ in appearance from females in that they have *D. cancellata* characters, whereas the females have *D. novopaca* characters. This contention is further supported by the fact that the one male produced in the reciprocal ♀ *D. novopaca* × ♂ *D. cancellata* cross had *D. novopaca* characters.

The situation can be further analysed in the ♂ *D. novopaca* × ♀ *D. cancellata* hybrids for here it was possible to backcross the F_1 females to both *D. novopaca* and *D. cancellata* males. From the former cross all progeny show *D. novopaca* characters and from the latter *D. novopaca* or *D. cancellata* characters with no recombination. This indicates that one gene or closely linked genes which are situated in the sex chromosome (as shown above) control thoracic pattern, abdominal markings, and clouding over crossveins.

V. Acknowledgments

Grateful acknowledgment is made to Professor W. Stephenson, Department of Zoology, University of Queensland, for helpful advice and criticism, and to Miss J. C. Browne for technical assistance.

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A RE-EXAMINATION OF THE MECOPTEROID AND ORTHOPTEROID FOSSILS (INSECTA) FROM THE TRIASSIC BEDS AT DENMARK HILL, QUEENSLAND, WITH DESCRIPTIONS OF FURTHER SPECIMENS

By E. F. Riek*

(*Manuscript received September* 6, 1955)

Contents

Summary

This paper interrelates the species of mecopteroid and orthopteroid insects (excluding Blattaria), described in the literature, from the Triassic beds at Denmark Hill, Queensland. The affinities of a number of the species are considered to be very different from those proposed in the original descriptions. A new genus of Planipennia and another of Gryllacrididae (Orthoptera) and a new species of Perlaria are described. The order Paratrichoptera Tillyard is relegated to family rank within the suborder Eumecoptera.

Introduction

Tillyard published a number of papers (1916, 1917, 1918, 1919, 1922, 1923, 1926) dealing with the insect fauna of this horizon of the Triassic Ipswich Series. This paper attempts to interrelate the species of mecopteroid and orthopteroid insects scattered throughout his papers. A number of additional specimens has been obtained since Tillyard's last paper and descriptions of these are included. Some of them are from the original Dunstan Collection but others are of more recent collecting by the staff of the Geology Department, University of Queensland, and the author. Two of these latter specimens come from a slightly different horizon separated by three or four hundred yards from the original site. Both specimens, wings of rather large insects, are beautifully preserved, so that the horizon is worthy of further development in the future.

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Very few Mecoptera are recorded from these beds and Trichoptera have not previously been recognized, though one of the described species, *Stereochorista frustrata* Tillyard, belongs in that order. The order Paratrichoptera is considered as a family, Mesopsychidae, within the Eumecoptera and the Protomecoptera, as represented by *Archipanorpa* Tillyard from this bed, has doubtful mecopteroid affinities. There are representatives of only two families of Eumecoptera, the Mesopsychidae referred to above and the Mesochoristidae. The Mesochoristidae persist from the Upper Permian, but are represented here only by the type genus *Mesochorista* Tillyard. The Mesopsychidae, which have a peculiar development of costal veinlets, are considered as a derivative of the Upper Permian Belmontiidae, although they have only a simple *CuA* in the forewing.

Four genera of Planipennia, here placed in two families, the Osmylopsychopidae and the Psychopsidae, were described by Tillyard. The latter family contains several Recent genera and is best developed in Australia. It is surprising that none of the Permian types of Neuroptera similar to those found at Belmont, New South Wales, have been described from these beds. However, in some of the unworked material uncovered at the original site, a species of *Archeosmylus* Riek does occur. At the new fossiliferous locality, a few hundred yards from the original site, which, however, is possibly not contemporaneous, another beautifully preserved osmylopsychopid has been discovered.

The orthopteroid insects described from these beds are placed here in the orders Protorthoptera, Orthoptera, and Phasmodea. A consideration of the order Blattaria, which is also well represented, is not included in this paper. A species of Perlaria is described in this revision. This is the first record of Perlaria from Triassic beds in Australia though not the oldest record of the order. However, the species is considered congeneric with the one described by Tillyard from the Upper Permian of Belmont.

Order MECOPTERA

Family MESOCHORISTIDAE

Genus MESOCHORISTA Tillyard

Mesochorista Tillyard, 1916, Qd. Geol. Surv. Publ. 253: 29.

Genotype *Mesochorista proavita* Tillyard, 1916, op. cit.: 30.

Primitive Mecoptera, forewing with a 2-branched *Sc*, 4-branched *Rs*, and 6-branched *M*, branching of *M* sometimes reduced to 5. In the hindwing *M* is only 4-branched.

MESOCHORISTA PROAVITA Tillyard

Mesochorista proavita Tillyard, 1916, Qd. Geol. Surv. Publ. 253: 30.

Type.—No. 32*a* (F39231 of the Australian Museum Collection). Counterpart No. 32*b* in the Dunstan Collection.

A second specimen (F39230 and counterpart F39271), in the Australian Museum, here referred to this species, shows overlapping fore and hindwings. In the forewing *M* is only 5-branched, with an extra fork on M_2 only, and in the hindwing *M* is only a 4-branched.

Tillyard's figure of the type is accurate in most respects, but he omits the crossveins of the radial and median fields. Actually there are no crossveins from *Sc* to the costal margin. The lettering of his figure is not accurate as *CuA* is shown as the posterior branch of *M*.

Family **ORTHOPHLEBIIDAE**

There is a rather fragmentary specimen, F39232 in the Australian Museum Collection, which belongs to this family. The specimen lacks most of the basal and apical thirds and also the anal field. It preserves an extra fork on R_2, giving a 5-branched *Rs*, and an extra fork on M_4.

Family **MESOPSYCHIDAE** Tillyard

Tillyard (1919) based his order Paratrichoptera on the single genus here placed in this family. It has a simple *CuA*, unlooped anal veins, and differs from most Mecoptera only in the series of costal veinlets, so the order cannot be maintained and the family Mesopsychidae must be placed in the Eumecoptera.

The family Pseudopolycentropodidae, incorrectly assigned to the Paratrichoptera by Martynov (1927) has a very different structure and is in no way related to the Mesopsychidae. The family Liassophilidae (Tillyard 1933) differs in having 3*A* looped on to 2*A* and in all of the anals being longer. Martynov (1937) has placed many quite distinct forms in this order.

Forewing: *Rs* and *M* both 4-branched; *Sc* branched and with a series of costal veinlets, otherwise normal Mecoptera.

Hindwing: Similar to forewing but *Sc* shorter and with fewer veinlets, and without a distinct cubito-median *Y*-vein.

The slight crinkling of the wing membrane is rather similar to that seen in the Belmontiidae (Riek 1953) but the family differs from the Paramecoptera in the unforked nature of *CuA* in the forewing. The two families show further similarities in the presence of costal veinlets, very large cubito-median *Y*-vein, and almost identical structure of *Cu* and anals, except for the forked *CuA*.

Genus MESOPSYCHE Tillyard

Mesopsyche Tillyard, 1917, Proc. Linn. Soc. N.S.W. 42: 181.
Triassopsyche Tillyard, 1917, Proc. Linn. Soc. N.S.W. 42: 182.
Aristopsyche Tillyard, 1919, Proc. Linn. Soc. N.S.W. 44: 200.
Neuropsyche Tillyard, 1919, Proc. Linn. Soc. N.S.W. 44: 203.

Genotype *Mesopsyche triareolata* Tillyard, 1917, Proc. Linn. Soc. N.S.W. 42: 182.

Not only are the four genera of Tillyard regarded as synonymous but their respective type species are considered conspecific. The type species of *Mesopsyche* is based on a hindwing. *Triassopsyche* is here considered to be a forewing in the same genus. *Aristopsyche* is a more complete forewing; Tillyard's figure shows a true costal vein, which, however, is really the humeral crossvein and two other crossveins brought into chance alignment. The specimen shows the normal structure of *CuA*, with distinct crossveins to *CuP* and to M_{3+4}. *Neuropsyche* is based on another very incomplete hindwing. In *Mesopsyche*, Tillyard has shown *CuA* and *CuP* fused towards the base, but in reality the veins are brought together only through a buckling of the wing membrane. In *Triassopsyche* R_1 is forked near the apex. There is no evidence of a crossvein to R_2 as figured by Tillyard.

Generic Diagnosis—Forewing: Normal Mecoptera except for a series of costal veinlets; *Rs* and *M* both normally 4-branched; a distinct cubito-median *Y*-vein. Sometimes there are small end-twiggings on the branches of *Rs*.

Hindwing: *Sc* shorter than in the forewing; without a distinct cubito-median *Y*-vein.

MESOPSYCHE TRIAREOLATA Tillyard

Plate 1, Fig. 1

Mesopsyche triareolata Tillyard, 1917, Proc. Linn. Soc. N.S.W. 42: 182.
Triassopsyche dunstani Tillyard, 1917, Proc. Linn. Soc. N.S.W. 42: 184.
Aristopsyche superba Tillyard, 1919, Proc. Linn. Soc. N.S.W. 44: 202.
Neuropsyche elongata Tillyard, 1919, Proc. Linn. Soc. N.S.W. 44: 204.

Types.—Types of all species in the Australian Museum, Sydney.

The above synonymy is based on an examination of the holotypes and three other specimens from the same beds and an almost perfect hindwing (C2247 and counterpart C2246, University of Queensland, Department of Geology Collection), with a length of 17 mm, from the new outcrop at Denmark Hill.

INCERTAE SEDIS

Suborder PROTOMECOPTERA Tillyard

Family ARCHIPANORPIDAE Tillyard

Genus ARCHIPANORPA Tillyard

Archipanorpa Tillyard, 1917, Proc. Linn. Soc. N.S.W. 42: 191.

Genotype *Archipanorpa magnifica* Tillyard, 1917, loc. cit.

ARCHIPANORPA MAGNIFICA Tillyard

Archipanorpa magnifica Tillyard, 1917, Proc. Linn. Soc. N.S.W. 42: 191.

Types.—Holotype No. 120*a*, paratype No. 106*a*, in the Queensland Geological Survey.

The affinities of this species are very doubtful. The presence of a free *C* would seem to exclude it from the Mecoptera, or possibly even from the mecopteroid stock.

Order TRICHOPTERA

Family STEREOCHORISTIDAE Tillyard

Tillyard placed this family in the Mecoptera. However, the species on which he based the family is a trichopteron, showing a forked *CuA* and, as an additional guide, with R_{2+3} forking before R_{4+5}, which occurs commonly in Trichoptera. Tillyard's figure and interpretation of the venation show the specimen upside down, the anterior border being interpreted as posterior, so that his R_3 to M_{4b} should read CuA_1, M_4, M_3, M_2, M_1, R_5, R_4, R_3, R_2. The specimen is in a very crushed state, particularly over the anterior portion, and the apical half has been pushed over the basal slightly at the break of *R* (Cu_1 of Tillyard), so that its affinities within the Trichoptera are doubtful and for that reason the Trichoptera of other Mesozoic beds have not been referred to it.

Genus STEREOCHORISTA Tillyard

Stereochorista Tillyard, 1919, Proc. Linn. Soc. N.S.W. 44: 196.

Genotype *Stereochorista frustrata* Tillyard, 1919, op. cit.: 197.

STEREOCHORISTA FRUSTRATA Tillyard

Fig. 1

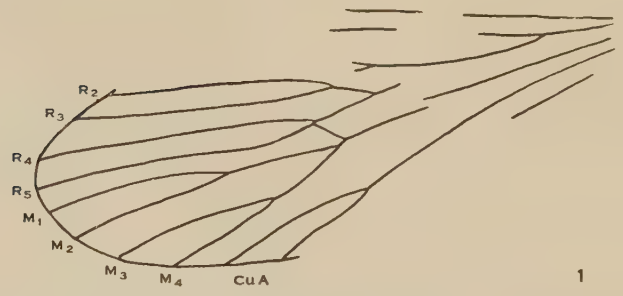


Fig. 1.—*Stereochorista frustrata* Tillyard. Free-hand drawing of the holotype.

Stereochorista frustrata Tillyard, 1919, Proc. Linn. Soc. N.S.W. 44: 197.

Type.—No. 218 in the Queensland Geological Survey.

The figure is a free-hand drawing of the type. A rough hand drawing is included as a camera lucida was not available when the type was examined in the Queensland Geological Survey.

Order PLANIPENNIA

Family ARCHEOSMYLIDAE

Genus ARCHEOSMYLUS Riek

Archeosmylus Riek, 1953, Rec. Aust. Mus. 23: 85.

Genotype *Archeosmylus pectinatus* Riek, 1953, op. cit.: 86.

This genus was known previously from the Upper Permian at Belmont and from the Triassic at Mt. Crosby. A primitive neuropteron from these Denmark Hill beds is placed in the same genus. This specimen, F39249 of the Australian Museum, is rather fragmentary and not worthy of specific description, though the record of the family in this Triassic horizon is of interest.

Family OSMYLOPSYCHOPIDAE

The genera of this family have hitherto been considered in the Prohemerobiidae. Three of the described genera of Planipennia were placed in that family, though one was subsequently removed to the Psychopsidae (Tillyard 1922). Although very fragmentary, it seems best to place the latter in the Osmylopsychopidae. A new genus, described in this paper, is also placed in this family, making the fourth from these beds.

Genus PROTOPSYCHOPSIS Tillyard

Protopsychopsis Tillyard, 1917, Proc. Linn. Soc. N.S.W. 42: 178.

Genotype *Protopsychopsis venosa* Tillyard, 1917, op. cit.: 180.

PROTOPSYCHOPSIS VENOSA Tillyard

Protopsychopsis venosa Tillyard, 1917, Proc. Linn. Soc. N.S.W. 42: 180.

Type.—No. 160*a* in the Queensland Geological Survey.

A very fragmentary specimen preserving only the apical third of the wing (length 9.5 mm). Its relationships are problematical but it is best considered in the family Osmylopsychopidae.

Genus OSMYLOPSYCHOPS Tillyard

Osmylopsychops Tillyard, 1923, Proc. Linn. Soc. N.S.W. 48: 496.

Genotype *Osmylopsychops spillerae* Tillyard, 1923, op. cit.: 497.

OSMYLOPSYCHOPS SPILLERAE Tillyard

Osmylopsychops spillerae Tillyard, 1923, Proc. Linn. Soc. N.S.W. 48: 497.

Types.—Holotype No. 314*a* and paratype No. 283*a* in the Queensland Geological Survey.

Length of wing from Tillyard's reproduction 40 mm. This species is based on two well-preserved fragments which show nearly the complete structure of the wing. Tillyard's reconstruction of the shape of the wing may not be correct as the postero-apical margin is not preserved.

Genus PETROPSYCHOPS, gen. nov.

Genotype *Petropsychops superba,* sp. nov.

Osmylopsychopid preserving clearly the apical structure of *Sc*, R_1, and *Rs* with *Sc* fused to R_1 and no distinct "vena triplica"; *R* bent strongly away from *Sc* at its base; *Rs* arising almost basally; *Cu* diverging strongly from the *Sc-R* veins; *M* forming a pectinate series of many anterior branches occupying a large area of the wing. The median field is most distinctive.

The genus is not closely allied to any of those already recorded from these beds, but in basal structures it approaches most closely to *Archepsychops* Tillyard, a genus placed in the Psychopsidae. The peculiar structure of *M* recalls that seen in the Jurassic Kalligrammidae.

PETROPSYCHOPS SUPERBA, sp. nov.

Plate 1, Fig. 2

Forewing: Almost complete except for apex and posterior margin; costal space moderately expanded, decreasing gradually towards the apex; *Sc* strong, fused to R_1 at its apex; R_1 diverging strongly from *Sc* at the base, strong, connected to *Sc* by spaced crossveins; *Rs* arising almost from base of *R*, immediately giving off a series of pectinate branches which, however, still show the dichotomic nature of their origin and form only a small angle with the stem of *Rs*; the more basad branches fork well before the middle, rather close to their origins; stems of *M* running parallel and close to *CuA*, giving off a large series of anteriorly directed pectinate branches which run almost parallel to the branches of *Rs*, so that without their basal attachments they would be considered as branches of that vein; *CuA* a very strong vein, diverging markedly from *Sc*, with a lower series of straight pectinate branches over its lower half; *CuP* arising almost basally and with several branches; several parallel branches to the anal veins. Length of specimen, along R_1, 28 mm.

Type.—Holotype C2136 and counterpart C2135 in the University of Queensland, Department of Geology Collection.

Type Locality.—Denmark Hill, near top of Ipswich series, Triassic. There is only the beautifully preserved holotype specimen.

Genus ARCHEPSYCHOPS Tillyard

Archepsychops Tillyard, 1919, Proc. Linn. Soc. N.S.W. 44: 205.

Genotype *Archepsychops triassica* Tillyard, 1919, op. cit.: 206.

ARCHEPSYCHOPS TRIASSICA Tillyard

Archepsychops triassica Tillyard, 1919, Proc. Linn. Soc. N.S.W. 44: 206.

Type.—No. 137*a* in the Queensland Geological Survey.

Tillyard first placed this genus in the Prohemerobiidae but subsequently (1922) removed it to the Psychopsidae. Its basal structures are

very different from those of *Triassopsychops* Tillyard of the Psychopsidae and, although the costal space is extremely wide near the base, it narrows markedly towards the apex. It seems best to place it in the Osmylopsychopidae.

Family PSYCHOPSIDAE

Subfamily TRIASSOPSYCHOPINAE Tillyard

Genus TRIASSOPSYCHOPS Tillyard

Triassopsychops Tillyard, 1922, Proc. Linn. Soc. N.S.W. 47: 467.

Genotype *Triassopsychops superba* Tillyard, 1922, op cit.: 469.

TRIASSOPSYCHOPS SUPERBA Tillyard

Triassopsychops superba Tillyard, 1922, Proc. Linn. Soc. N.S.W. 47: 469.

Type.—No. 284*a* in the Queensland Geological Survey.

Length of fragment 29 mm, indicating a total length of about 32 mm. This species differs from the other Ipswich Neuroptera in the structure of *Sc*, R_1, and *Rs* (forming a true "vena triplica"), and in the basal structure of *CuA*.

Order PROTORTHOPTERA

Family MESORTHOPTERIDAE Tillyard

Mesorthopteron Tillyard, 1916, Qd. Geol. Surv. Publ. 253: 14.

Genotype *Mesorthopteron locustoides* Tillyard, 1916, loc. cit.

MESORTHOPTERON LOCUSTOIDES Tillyard

Plate 2, Fig. 1

Mesorthopteron locustoides Tillyard, 1916, Qd. Geol. Surv. Publ. 253: 14.

Mesorthopteron locustoides Tillyard, 1922, Proc. Linn. Soc. N.S.W. 47: 448.

Types.—No. 5*a* and 5*b* in the Queensland Geological Survey. 5*c* does not belong (as stated by Tillyard 1922).

There are a number of additional specimens: Nos. 258*b*, 72*a-b*, 75, 78*a-b*, 123, 224, 234, and 241*b* in the Queensland Geological Survey; and, in the Australian Museum, F39242 preserving all but the anals and the apical third of the wing, and F39235 preserving only the apex.

The pectinate branches on *CuA* are distinctive. Many of the fragmentary specimens are associated, in part, on the primitive archedictyon.

Order ORTHOPTERA (SALTATORIA)

Family LOCUSTOPSIDAE Handlirsch

Genus TRIASSOLOCUSTA Tillyard

Triassolocusta Tillyard, 1922, Proc. Linn. Soc. N.S.W. 47: 451.

Genotype *Triassolocusta leptoptera* Tillyard, 1922, loc. cit.

This is the oldest genus of the family which is known also from the Liassic and Jurassic (Zeuner 1939).

Triassolocusta leptoptera Tillyard

Triassolocusta leptoptera Tillyard, 1922, Proc. Linn. Soc. N.S.W. 47: 451.

Triassolocusta leptoptera Zeuner, 1942, Proc. R. Ent. Soc. Lond. 11: 8.

Type.—Holotype No. 99 in the Queensland Geological Survey.

The stem of *Cu* and the anals are not preserved. There is a crossvein from M_{3+4} at its closest point to *Cu*, just after the forking of M_{1+2}. M_4 possibly shows a small terminal fork.

Family **TRIASSOMANTIDAE** Tillyard

Genus TRIASSOMANTIS Tillyard

Triassomantis Tillyard, 1922, Proc. Linn. Soc. N.S.W. 47: 450.

Genotype *Triassomantis pygmaeus* Tillyard, 1922, loc. cit.

Triassomantis pygmaeus Tillyard

Triassomantis pygmaeus Tillyard, 1922, Proc. Linn. Soc. N.S.W. 47: 450.

Type.—Holotype No. 86*a* in the Queensland Geological Survey.

The holotype differs somewhat from the text-figure given by Tillyard. The costal margin is straight, with a short *C* preserving only the apical half. The stem of *Cu* is not preserved but there is a fracture along that line. There are fewer apical forks to the vein designated as *M* with M_3 and M_4 remaining simple and M_2 possibly so. There are fewer anterior branches to R_3, possibly only two.

The relationship seems to be with the Geinitziidae and not at all with the Mantodea.

Family **GRYLLACRIDIDAE**

Subfamily **PROPARAGRYLLACRIDINAE**, subfam. nov.

Differing from Recent Gryllacrididae in the origin of *M* and in the fusion between *M* and *Cu*. *M* arising from the stem of *R* close to the base; stem of *M* fused with upper branch of *Cu*, with *M* forking distally after becoming free from *Cu*.

Genus PROPARAGRYLLACRIS, gen. nov.

Genotype *Proparagryllacris crassifemur*, sp. nov.

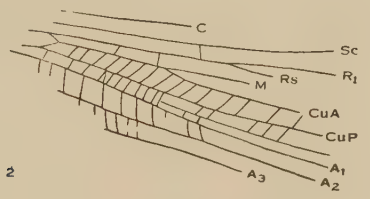
Forewing: Wing fragmentary, only discally preserved; with the characters enumerated above; branching of the veins similar to that of the Recent *Paragryllacris*, with *M* and *Cu* each 2-branched and with portions of these veins fused.

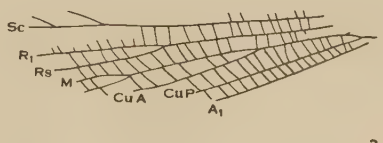
Proparagryllacris crassifemur, sp. nov.

Plate 2, Fig. 3; Figs. 2-3

Forewing: Costa only partly preserved; *Sc* with a distal upward curvature, with at least two anterior branches; *R* diverging somewhat from

Sc after the origin of *Rs*; apical portions of *R* and *Rs* not preserved; *M* arising from the stem of *R* close to the base, fused to *Cu* almost immediately, becoming free well before the origin of *Rs*, forking after the origin of *Rs*; basal origin of *Cu* not preserved, forking before the origin of *M*, upper branch fused to the stem of *M* just after its origin, lower branch (?*CuP*) remaining simple; 1*A*, 2*A*, and 3*A* widely separated basally, converging distad.





Proparagryllacris crassifemur, sp. nov.
Fig. 2.—F39251, holotype, × *c.* 3.
Fig. 3.—C2134, paratype, × *c.* 3.

Hindleg: Femur large and basally expanded; tibia at least as long as the femur, its apex not preserved.

Types.—Holoypte F39251, preserving portions of two wings, pronotum, and hindleg, in the Australian Museum Collection. Paratype C2134 in the University of Queensland, Department of Geology Collection. The paratype is more fragmentary than the type but preserves the anterior branches of *Sc* and the forking of *M* (length of fragment 16 mm).

Type Locality.—Dunstan Bed, Denmark Hill, Ipswich Series, Triassic.

The specimens, though fragmentary, preserve the essential basal structures, so that there can be no confusion of the species.

Order PERLARIA

Family EUSTHENIIDAE

Tillyard (1935) placed the genus *Stenoperlidium* Tillyard, originally recorded from the Permian of Belmont, in this family on a combination of wing venation and larval characters. A second species, described in this paper, shows additional primitive characters, but it is considered best to retain the genus within this family.

Genus STENOPERLIDIUM Tillyard

Antitaxineura Tillyard, 1935, Proc. Linn. Soc. N.S.W. **60**: 382.

Stenoperlidium Tillyard, 1935, op. cit.: 386.

Genotype *Stenoperlidium permianum* Tillyard, 1935, op. cit.: 387.

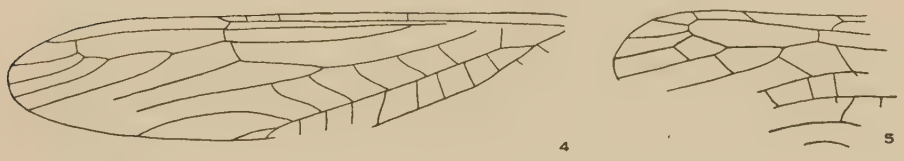
Stenoperlidium is considered as a possible synonym of *Antitaxineura* which was described in the Odonata, family Polytaxineuridae. *Antitaxi-*

neura is based on such a fragmentary specimen that it is best considered a nomen dubium and the name *Stenoperlidium* retained for this genus of Perlaria.

Forewing: Very narrow, not particularly narrowed basally; *Sc* rather short, ending a little beyond half-way in a short fork connecting with both *C* and R_1; costal veinlets only moderately well developed; *R* strongly built, *Rs* with a series of 4 pectinate branches distally; *M* 2-branched, forking just before half-way; *CuA* a strong vein divided into 3 distally; a strong crossvein from *CuA* to the stem of *M*; *CuP* unbranched.

STENOPERLIDIUM TRIASSICUM, sp. nov.

Plate 2, Fig. 2; Figs. 4-5



Stenoperlidium triassicum, sp. nov.
Fig. 4.—C2244, holotype, × *c.* 3.
Fig. 5.—F39256, paratype, × *c.* 3.

Forewing: Almost complete, length 27 mm, lacking most of anal veins, extreme base and apex not clearly preserved; *Sc* ending a little beyond half-way in a short fork connecting with both *C* and R_1 and touching R_1 just before a strong crossvein from *Rs*; crossveins from *Sc* to the costal border limited in number; R_1 strong, not clearly preserved in the pterostigmatic region; *Rs* 4-branched, arising at about one-fourth, gently convexed to R_1 as far as the end of *Sc* and there connected to R_1 by a strong crossvein, then diverging from R_1 again before branching; base of *M* not preserved (wing slightly crumpled); *M* 2-branched, the upper branch deflected towards *Rs* and connected to it by a strong crossvein at the level of the end of *Sc*; basal origin of *Cu* not preserved, stem forking early, a strong crossvein from *M* close to its origin to *CuA* close to its origin; the crossvein runs postero-distally, in a direction opposite to the cubito-median crossveins; *CuA* branches very close to its apex, 3-branched, with CuA_1 strongly arched towards *M*, CuA_2 arising almost at the wing margin and only slightly arched away from the margin, CuA_3 extremely short, continuing the direct line of *CuA* to the wing margin; *CuP* a weak vein, almost parallel to *CuA*; 1*A* only partly preserved, a strong simple vein; other anals not preserved; distinct oblique crossveins running in different directions between *M* and *CuA* and between *CuA* and *CuP*.

Type.—Holotype C2244 and counterpart C2245 in the University of Queensland, Department of Geology Collection.

Type Locality.—New outcrop, Denmark Hill, near top of Ipswich Series, Triassic.

There is a second specimen, F39256 in the Australian Museum Collection from the Dunstan locality, preserving the apical third of a wing. In this specimen *Sc* ends a little earlier, the branching of *Rs* differs in detail and the apical branching of *CuA* is more distinct. The apex is slightly more rounded. In all probability it is the apex of a hindwing.

This species can be distinguished by the branching of *CuA*, the shape of the stem of *Rs*, and the more angled M_{1+2}. It is close to the genotype and preserves more of the basal structure of the wing, particularly the forking of *Cu* and the cubito-median *Y*-vein, which shows clearly the direction of the median arm.

Order PHASMODEA

The family Aeroplanidae placed by Tillyard (1918) in a distinct suborder Aeroplanoptera of the Protodonata is considered to fall within this order. Martynov (1928) also considers this family in the Phasmodea. He places the Aeroplanidae, the Necrophasmidae, the Aerophasmidae, and the Chresmodidae in the suborder Chresmododea.

Suborder CHRESMODODEA

Family AEROPLANIDAE Tillyard

Genus AEROPLANA Tillyard

Acroplana Tillyard, 1918, Proc. Linn. Soc. N.S.W. **43**: 426.

Genotype *Aeroplana mirabilis* Tillyard, 1918, loc. cit.

AEROPLANA MIRABILIS Tillyard

Aeroplana mirabilis Tillyard, 1918, Proc. Linn. Soc. N.S.W. **43**: 426.

Type.—Holotype No. 126*a* in the Queensland Geological Survey.

This species shows a very primitive condition, with a well-developed forewing, apparently as long as the hindwing. The anal fan of the hindwing is very imperfectly preserved but it can be seen on the lower side of the holotype specimen.

This is the oldest representative of the order. The Necrophasmidae and the Aerophasmidae are from the Upper Liassic of Turkestan and the Chresmodidae are from the Upper Jurassic of Bavaria and England.

INCERTAE SEDIS

Genus MESOMANTIDION Tillyard

Mesomantidion Tillyard, 1916, Qd. Geol. Surv. Publ. **253**: 16.

Genotype *Mesomantidion queenslandicum* Tillyard 1916, loc. cit.

MESOMANTIDION QUEENSLANDICUM Tillyard

Mesomantidion queenslandicum Tillyard, 1916, Qd. Geol. Surv. Publ. 253: 16.

Type.—Holotype 1*a* in the Queensland Geological Survey, 1*b* (counterpart) in the Dunstan Collection.

This is not considered to be an insect, but if it is, its relationships are very problematical.

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FOSSIL INSECTS FROM TRIASSIC BEDS

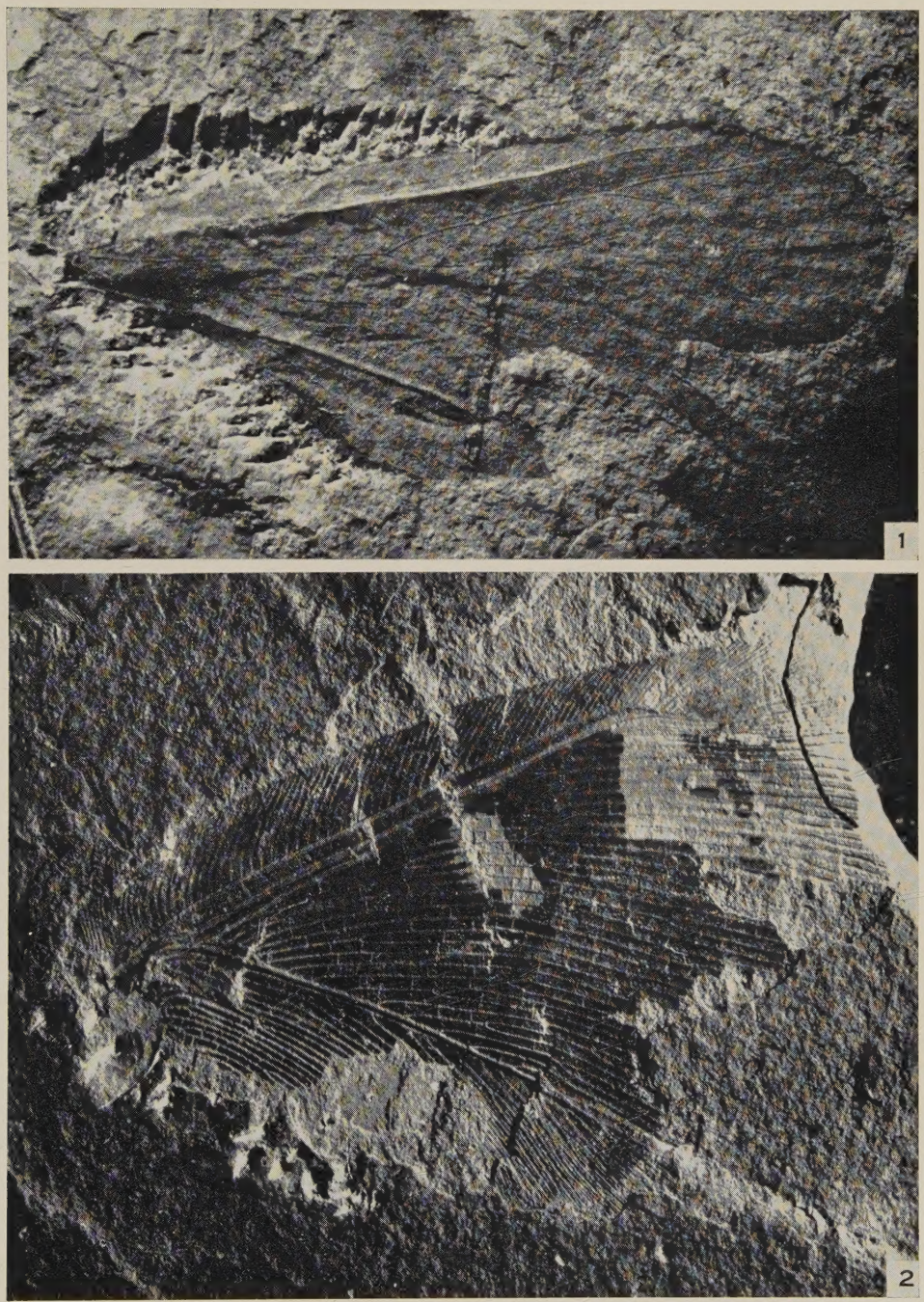

Fig. 1.—*Mesopsyche triareolata* Tillyard, hindwing, C2247. × *c.* 7.
Fig. 2.—*Petropsychops superba*, gen. et sp. nov., holotype, C2136. × *c.* 4.

FOSSIL INSECTS FROM TRIASSIC BEDS

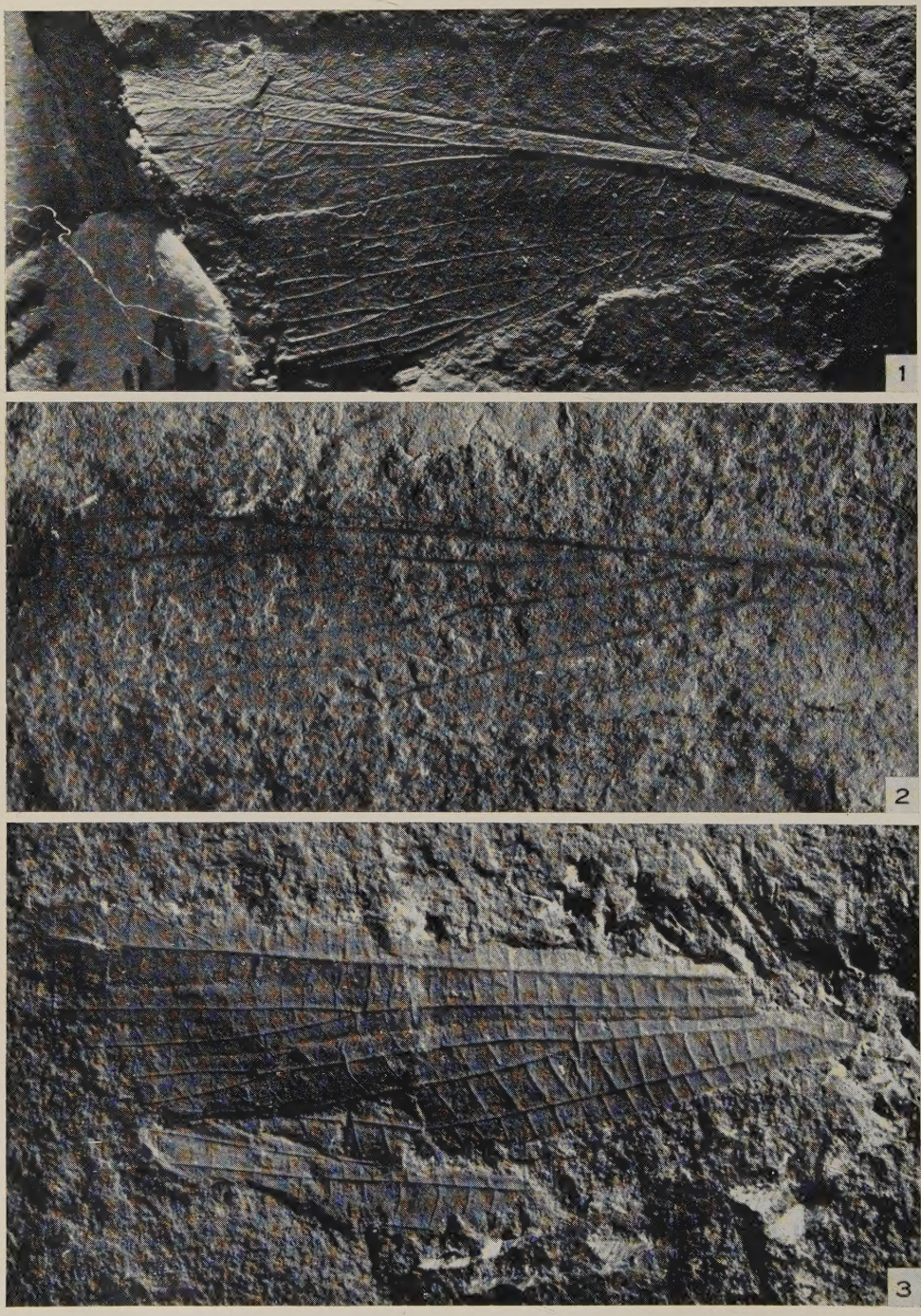

Fig. 1.—*Mesorthopteron locustoides* Tillyard, F39242. × *c.* 5.
Fig. 2.—*Stenoperlidium triassicum*, sp. nov., holotype. C2244. × *c.* 4.
Fig. 3.—*Proparagryllacris crassifemur*, gen. et sp. nov., paratype, C2134. × *c.* 6.